

Thermoregulation in the Brown Water Snake, Natrix taxispilota,
with Discussion of the Ecological Significance of
Thermal Preferenda in the Order Squamata

By

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This work is dedicated to my parents, Arvil E. Goodman and Clara Metcalf Goodman, who encouraged my pursuit of biology in general and snakes in particular.

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Abstract of Dissertation Presented to the Graduate Council
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THERMOREGULATION IN THE BROWN WATER SNAKE, NATRIX TAXISPILOTA,
WITH DISCUSSION OF THE ECOLOGICAL SIGNIFICANCE OF
THERMAL PREFERENDA IN THE ORDER SQUAMATA

By

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Thermoregulatory behavior of the brown water snake, Natrix taxispilota, was studied under natural and laboratory conditions. During daylight hours, snakes move among shade, sun, and water to maintain their preferred body temperature. In the evening they submerge regardless of air-water temperature differential and spend the night in the water. There are minimal thermal thresholds for morning emergence and these levels are affected by thermal acclimation and physiological state of the animal.

The preferred range of body temperatures of this species decreases with increasing acclimation temperature. When digesting food, snakes thermoregulate within a sub-range of the normal preferred range and digestive extraction efficiency is greatest at this level -- about 30°C.

It is suggested that high thermal extremes are selective forces which directly fix the critical thermal maximum of reptiles and indirectly fix the preferred body temperature. The relatively low thermal preferenda of snakes may be a function of their lack of limbs which precludes thermoregulation with the degree of independence of conductive heat exchange with the substrate characteristic of lizards.

INTRODUCTION

Many species of reptiles utilize solar radiation to attain body temperatures greatly in excess of ambient temperatures. Some species have an extensive behavioral repertoire which enables them to regulate their body temperature within fairly narrow limits. Since these initial discoveries were reported (Cowles and Bogert, 1944), scores of papers have appeared documenting such behavior for other reptilian species, and it now seems obvious that thermoregulation is a general feature of reptilian behavior. While some reptiles possess physiological mechanisms that contribute to thermal homeostasis (Lueth, 1941; Cole, 1943; Cowles, 1958; Ruibal, 1961; Bartholomew and Tucker, 1963; Heath, 1965; Hutchison et al., 1966; Kour and Hutchison, 1970; Weathers, 1970), it is behavioral utilization, directly or indirectly, of solar radiation that permits the attainment of high preferred thermal levels. The contribution of metabolic heat to maintenance of thermal homeostasis is negligible (Lueth, 1941; Cole, 1943; Mackay, 1964; Schmidt-Nielsen and Dawson, 1964; Brattstrom, 1965) even in large reptiles.

With few exceptions, these studies have dealt with lizards, and very little information exists for other reptilian groups. The few studies of thermoregulation involving snakes (Cowles and Bogert, 1944; Carpenter, 1956; Fitch, 1956, 1965; Brattstrom, 1965; Stewart, 1965; Myres and Eells, 1968; Kitchell, 1969; McGinnis and Moore, 1969; Osgood, 1970) indicate that snakes differ from lizards in their thermal behavior. They seem to have lower thermal preferenda and to regulate less precisely. Some workers (Cowles and Bogert, 1944; Schmidt-Nielsen

and Dawson, 1964) believe these differences are correlated with differences in the ecology of the two groups. Most snakes, for instance, are nocturnal or crepuscular and many are fossorial; lizards are mostly diurnally active and terrestrial. Even among nocturnal and fossorial reptiles, however, basking in the sun has been either regularly or occasionally reported (Cowles and Bogert, 1944; Bailey, 1949; Brattstrom, 1952). The significance of diurnal thermoregulation in such forms has never been explored.

This study was undertaken to determine the significance of thermoregulation in a species of snake which is both semi-aquatic and nocturnally active. Natrix taxispilota, the brown water snake, spends nights in the water of large open lakes or rivers and springs. During the daylight hours of the warmer months, the species commonly lies on limbs overhanging the water, either in the sun or in the shade. Except for reproductive behavior in the early spring, little activity occurs during the day. This snake almost never occurs away from the water's edge, and the aerial phase of its existence is limited to basking on vegetation, rather than shore. While lying above the water, the snake is surrounded by a thermal medium that is virtually homogeneous, and heat exchange is largely radiative. Convective heat exchange there is minimal because snakes remain in the water on windy days. Heat exchange during the aquatic stage of the activity cycle, however, is almost completely conductive. Because the species' activity is partitioned almost completely between these two phases -- nocturnal aquatic activity and diurnal arboreal basking -- it seems an ideal snake for a study of the mechanisms and significance of thermoregulation.

MATERIALS AND METHODS

Collection and Maintenance of Specimens

Almost all the snakes used for this study were collected at Newnan's Lake, 8.7 km east of Gainesville, Alachua County, Florida. This 2390 hectare lake has a mean depth of two m and is bordered by trees, particularly pond cypress Taxodium ascendens and water ash Fraxinus caroliniana, both of which extend from the shoreline out for as much as 20 m into the lake. It is at the interface of the lake and the outermost trees that most of the Natrix taxispilota were found basking. Animals used in laboratory studies were collected by hand from a motorboat. Cloacal temperature was recorded at this time with either a Schultheis thermometer or the thermister probe of a YSI six-channel tele-thermometer. Air temperature was taken in the shade at the time of capture and water temperature was recorded at the surface and at a depth of 2/3 m. A black-bulb temperature was recorded in direct sunlight with a mercury thermometer, the bulb of which had been coated with flat black paint.

A 1.12 km section of shoreline was used as a census area and, at irregular intervals, the number of snakes basking in the trees of this area was recorded. These surveys were always conducted between 1300 and 1500 hours EST. On a few days, censuses for this and other areas were taken at hourly intervals between 0700 and 1830 hours EST to determine the extent of temporal variation in the number of basking individuals. Associated air, water, and black-bulb temperatures were recorded during censusing, and general weather conditions were noted.

Snakes used for thermal gradient, digestive efficiency, and metabolic experiments were acclimated prior to use. Each animal was housed in a plastic storage container with holes in the removable lid. These containers were placed in a Jewett environmental cabinet, a Forma model 13 incubator, or a Lab Line controlled environmental room where the temperature was maintained within $.5^{\circ}\text{C}$. All snakes received 12 hours of light daily (0900-2100 hours EST) and had water continuously available in dishes which were too small to permit submergence of snakes weighing more than 100 g.

Radio Telemetry

Ingestible blocking oscillator radio transmitters were used to obtain snake body temperatures under experimental conditions. The broadcast frequency used was low enough (500-1000 kc) to permit the reception of both aerial and underwater signals generated within 2 m of the receiver, an AM-FM portable radio. Antennal loops were always necessary to relay the signal to the receiver.

Each cylindrical (radius = 7.5 mm, length = 57 mm) transmitter was powered by a replaceable 1.5 volt silver oxide hearing aid battery and was waterproofed with a thin coat of 1:1 mixture of beeswax and paraffin. The transmitter was lubricated, forced into the throat of the snake and massaged by hand to the stomach (Fig. 1). The transmitter was regurgitated in four or more days depending on temperature. Transmitters were calibrated immediately before and after use.

Experimental Apparatus

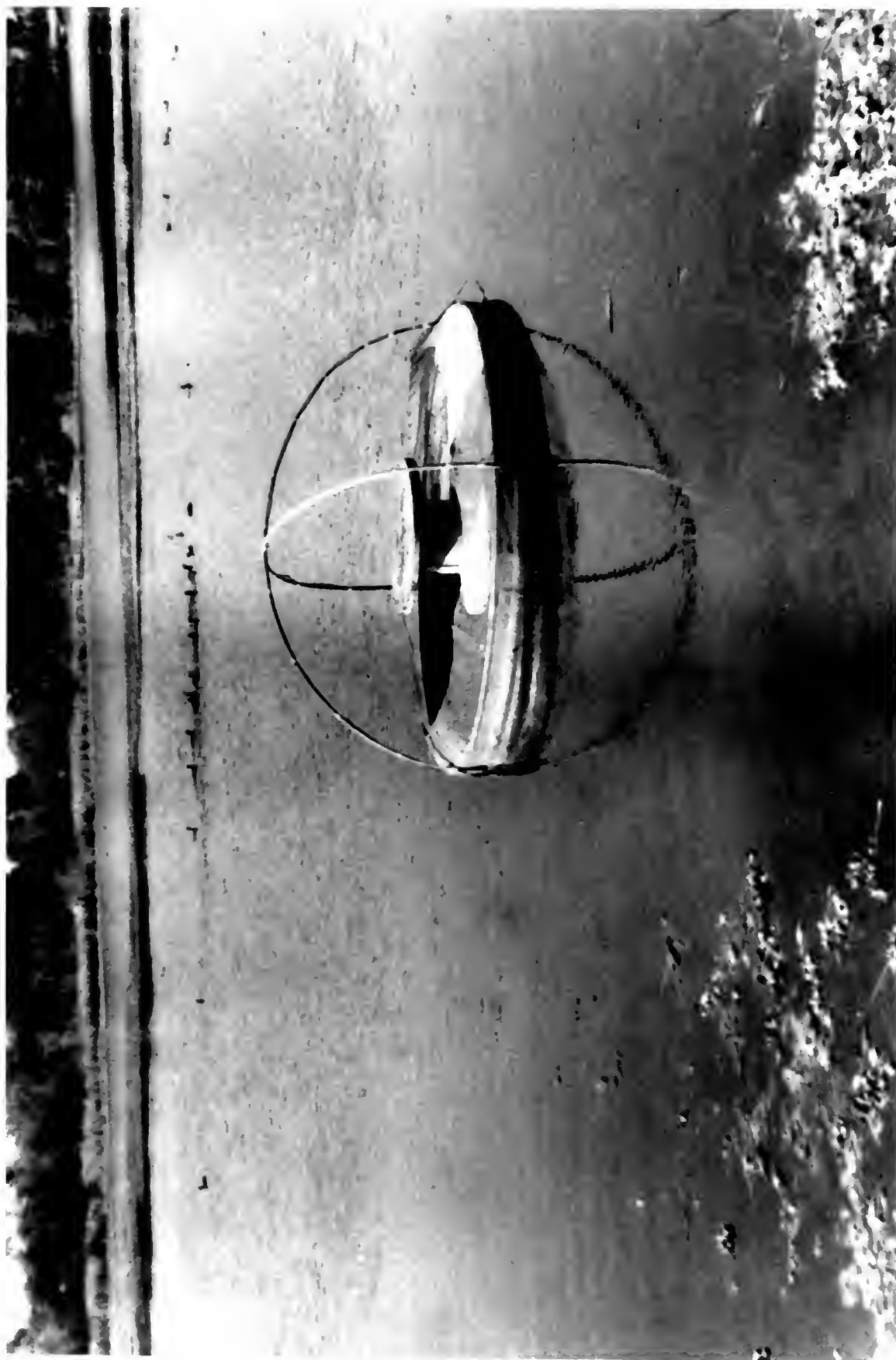
To study the fluctuations of body temperatures with changing environmental temperatures, an experimental pen was built at another nearby location, Lake Alice. This 24-hectare lake is located on the University of Florida campus. The pen consisted of a circular galvanized steel cattle watering trough 2.44 m in diameter and 61 cm high. Concrete

Figure 1. X-ray photograph of a Natrix taxispilota with
an ingestible radio transmitter in its stomach.



blocks were stacked in the center of the trough to a level of about 50 cm and a wooden cable spool 76 cm in diameter was placed on its side atop the blocks. An antennal loop system was installed so that radio transmitter signals could be monitored at a distance from the pen. This consisted of a 25-m section of insulated copper cable ringing the pen in three perpendicular planes. Two loops, therefore, passed under and over the spool and their components extending above the rim of the pen were supported by arched sections of screen moulding (Fig. 2); the third loop was situated along the inside periphery at the rim. The ends of this antennal loop were connected to a 20-m section of insulated copper wire which was connected by insulated tip plugs to the antenna of a portable AM-FM radio. Signals generated anywhere inside the loop could thus be monitored many meters away. A 1/4-inch mesh hardware cloth retaining fence was attached to the top edge of the trough and directed inward toward the center of the pen to prevent the escape of snakes. This apparatus was floated into the lake and filled with water to the level of the bottom of the wooden spool. The free-floating pen was then anchored and the wire connecting the antennal loop to the radio was sunk to the bottom between the pen and the shore. Snakes used in this phase of research were introduced into the pen and allowed several days to adjust to their environment. They were then force-fed an ingestible transmitter. On sunny days, the snake had both sunny and shaded basking sites available on the wooden spool, or it could remain underwater in the cavities of the concrete blocks. Air, water, and black-bulb temperatures were monitored with either a YSI telethermometer located on shore or with mercury bulb thermometers. In trial determinations, the water temperature inside and outside the pen never differed by more than 1.5°C. The water inside was sometimes

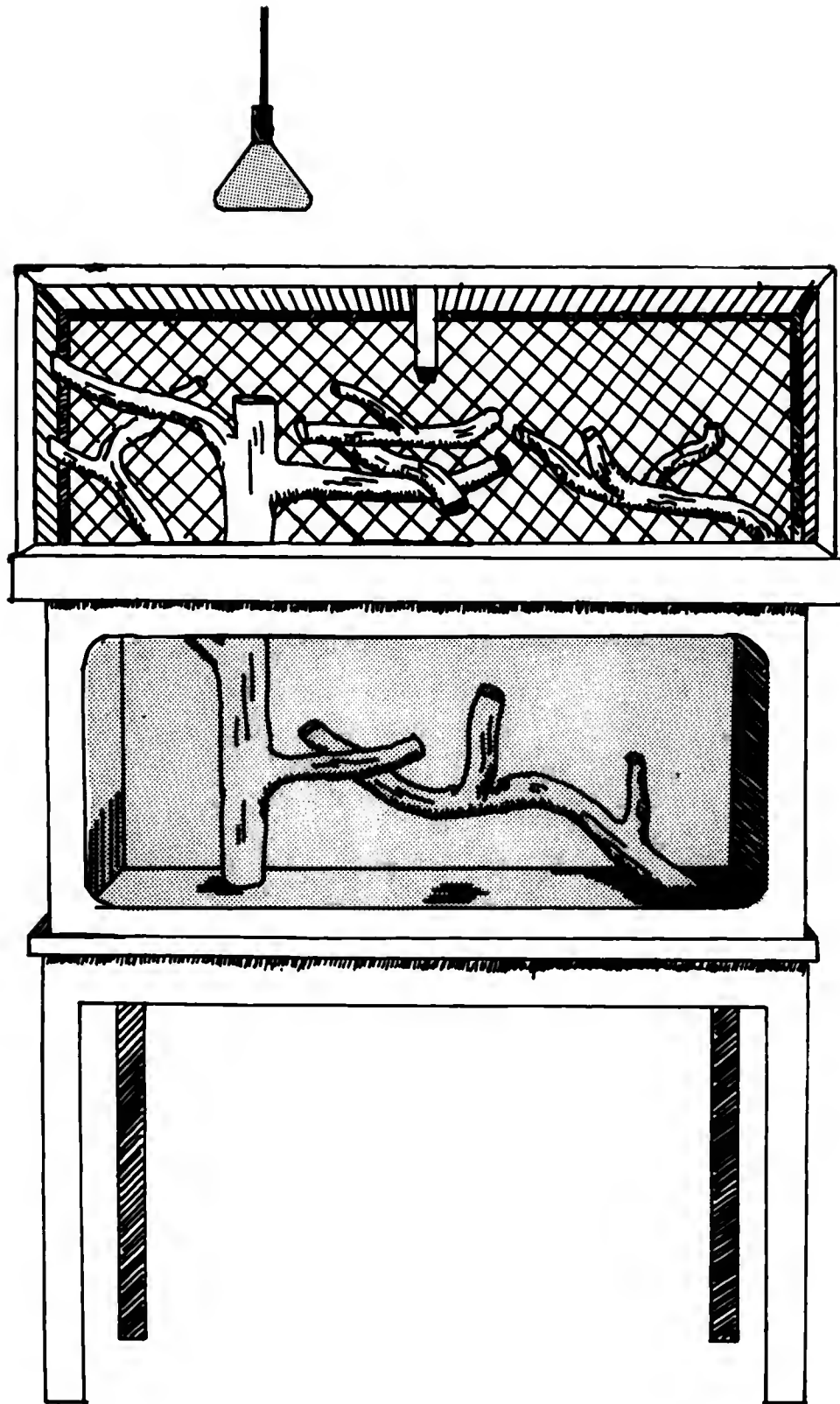
Figure 2. Experimental pen at Lake Alice.



slightly cooler, presumably because of the shade provided by the vertical sides of the pen. Observations were made from the shore either with the naked eye or through 30 X binoculars, depending upon the distance separating the observer and the pen.

A laboratory apparatus was used to study thermoregulatory behavior under more controlled conditions. A 230 liter aquarium was made by sealing a refrigerator liner, cutting a large window in one side and sealing in a section of reinforced glass. Water temperature was controlled by circulating water between the aquarium and a Forma constant temperature water bath. A bottomless wood-frame 1/4-inch mesh cage (90 cm X 70 cm X 40 cm) with sliding glass panels in front. was placed above the aquarium, and Sambucus limbs were wired into positions both underwater and above water to provide the snakes with numerous resting and basking sites. A 250 watt infrared heat lamp was placed directly above the right side of the cage about 20 cm above the highest basking site. A wooden partition was hung from the top of the cage; this did not restrict movement but rather shaded the left side of the cage from "sunlight" (Fig. 3). Caged animals could thus either remain submerged or bask aerially in the "sun" or shade. This aquarium-cage-water bath combination was placed inside a Lab Line controlled environmental room which maintains temperatures between -20 and 70°C within .5°C. Water, air and black-bulb temperatures were monitored with a YSI tele-thermometer placed outside the room. The probes were placed inside the aquarium pen in the water, shaded air and approximately 20 cm directly below the sunlamp respectively. The black-bulb probe was coated with flat black paint. Ingestible transmitters were used to monitor body temperatures. A three-plane antennal loop was placed in the aquarium cage and leads were extended outside the room to the antenna of an AM-FM radio. All

Figure 3. Experimental chamber used to determine the responses of water snakes to various combinations of air and water temperature.



observations were made through two 10 cm X 6 cm holes in a sheet of brown paper which covered the glass door of the environmental room. With this apparatus, air and water temperatures could be monitored and varied independently, the snake's behavioral adjustments could be observed and its body temperature recorded without disturbing the animal.

Responses of the animals were recorded for all combinations of air and water temperatures from 5° through 35°C. A timer was attached to the environmental room and a 12-hour light cycle (0900-2100 hours EST) was used throughout. Because of the nature of the transmitter used, it was difficult to separate two signals; consequently one animal, a 554 g female, was used for all determinations. Numerous individuals were later run at selected temperature combinations to verify the generality of responses of this individual. The female used in this experiment was not acclimated to any particular temperature because reacclimation after each run would have prolonged the experiment by many months. Also, the temperature combination changes were never drastic. Usually the water temperature remained constant while all air temperatures from 5°C through 35°C were run. Each combination was run for two hours and then the air temperature was elevated 2°C. Since these temperature changes were gradual, there is no reason to believe that the snakes used in this experiment were acclimated to temperatures to which they would not ordinarily be acclimated under the same thermal conditions in the wild.

Thermal Gradient

A thermal gradient was used to determine preferred body temperature levels in this species. The gradient consisted of a rectangular open-top wooden box 3.35 m long, 30 cm wide and 30 cm high with a nickel-steel

alloy floor. The front of the box was marked at 5 cm intervals from the hot to the cool end. At the cool end, a bottomless one-gallon aluminum can was cemented to the floor of the gradient and filled 2/3 full of water. Cold water was then circulated through a coiled section of copper tubing in the can. Heat was provided at the other end by an electric iron that was placed flat on the metal floor. A 500 ml beaker of water was placed beside the iron to maintain a high humidity inside the gradient. Panes of glass were placed on top of the gradient to prevent escape of snakes and to permit observation. A gradient with an average ΔT of 1°C per 30 cm between 20° and 34°C could be maintained indefinitely after an initial eight hour warm-up period. Acclimated snakes were force-fed ingestible transmitters at about 2100 hours, placed in the gradient, and left overnight for adjustment. Body temperature and location in the gradient were recorded at approximately 1-1/2 hour intervals between 0900 and 2400 hours of the following day. Snakes in the gradient received the same 12 hour photoperiod from overhead lighting as in their acclimation quarters. A red light was used when readings were taken during hours of darkness.

Metabolism

Metabolic rates were measured with a Beckman G-2 oxygen analyzer. Metabolic chambers consisted of 21.5 cm diameter glass battery jars 30.5 cm high, with holes drilled at low and high levels on the sides to let air in and out. A plexiglass lid with a 9.0 cm diameter hole for a size 15 rubber stopper was cemented to the top of the chamber. Acclimated snakes were introduced into the chamber which was then submerged in a controlled-temperature water-bath that maintained water temperature within $.5^{\circ}\text{C}$. Air was pumped through a coil of copper tubing that was submerged in the water bath before entering the chamber.

Oxygen consumption readings were taken at half-hour intervals until stable values were obtained.

Digestive Efficiency

The effect of temperature upon digestive efficiency was measured calorimetrically. A large number of gizzard shad, Dorosoma cepedianum, were collected by rotenone poisoning at Newman's Lake, and immediately frozen. In feeding experiments, fish were weighed, ground whole in a Waring blender and freeze-dried in a Virtis freeze-drying apparatus. The resulting mixture was ground again and filtered through 1/4-inch mesh screening to remove scales and large scale fragments. The resulting powder was thoroughly mixed and a .5 to 1.0 g sample removed for calorimetric determination in a Parr adiabatic oxygen bomb calorimeter. The remaining powder was rehydrated to the original wet weight calorimetric value and immediately fed to preweighed acclimated snakes at a level of .1 g per g of body weight. The food was massaged by hand to the snake's stomach and animals were then replaced in acclimation quarters and permitted to digest the meal at the temperature to which they were acclimated.

Cages were checked daily for defecation and the feces were rinsed out of the cages, collected in individual beakers and refrigerated. After digestion was completed (the cessation of defecation) the accumulated feces were either freeze-dried or vacuum dessicated and the dry feces weighed and bombed. At the temperatures of 20°C and above, snakes passed musk from the musk glands, the amount increasing with temperature. The quantity of musk per g of body weight was determined at the acclimation temperatures used and samples were bombed to determine calorimetric value. A correction for this factor was introduced into the calculations. Digestive efficiency is defined

here as:

$$E = 1 - \frac{C_f - C_m}{C_i}$$

where E = digestive efficiency; C_f = caloric value of feces; C_i = caloric value of ingested food; and C_m = caloric value of musk. Dried samples of fish, feces, and musk were weighed to the nearest .0001 gram on a Mettler H15 balance.

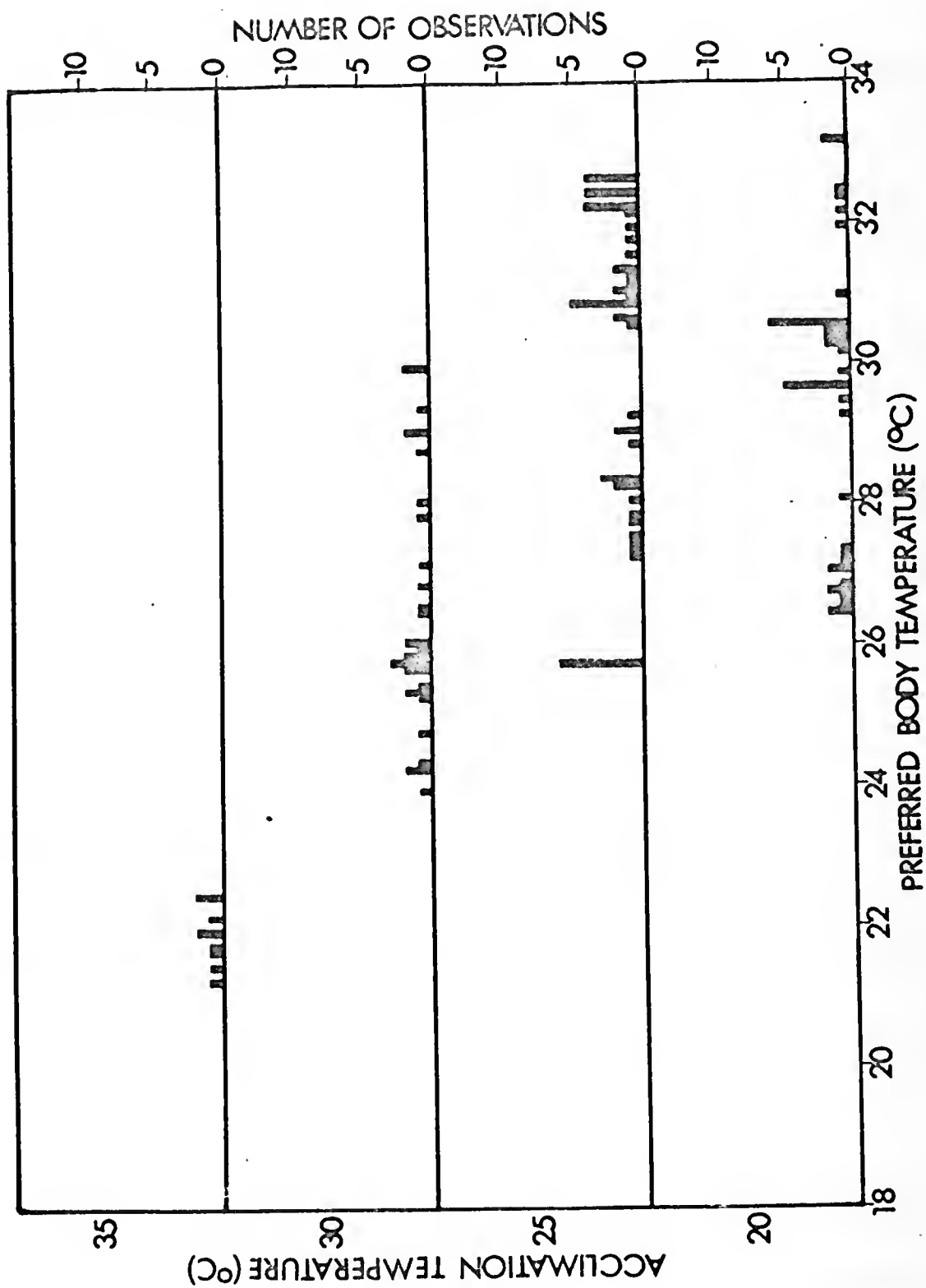
RESULTS AND DISCUSSION

Preferred Body Temperature

Throughout this discussion, the term preferred body temperature (abbreviated PBT) will be used in accordance with Peters (1964) who defined it as "that temperature at or about which all members of a reptilian species will maintain themselves given the opportunity to select proper substrate, exposure to sunlight, or other thermal factors." The PBT can thus refer to a thermal range, as initially defined (Cowles and Bogert, 1944) or to the mean of that range, the latter being more useful for comparisons of interspecific preferences.

The level of body temperature selected by Natrix taxispilota in a thermal gradient is inversely proportional to the temperature at which the snakes were acclimated (Fig. 4). This is consistent with the findings of Wilhoft and Anderson (1960) for Sceloporus occidentalis. The ecological significance of such interdependence is not immediately clear. It might be expected that PBT would be independent of acclimation as Licht (1968) found in Anolis, and serve as an immutable focal point for thermoregulatory behavior. In other vertebrate poikilotherms, similarly disparate results have been obtained. Rana pipiens tadpoles (Lucas and Reynolds, 1967) and many fish (Norris, 1963; Fry, 1964) show changes in PBT with acclimation, but the preferred thermal level of the newt Taricha rivularis cannot be shifted by acclimation (Licht and Brown, 1967). Thus, it is impossible to generalize about the capacity of vertebrate poikilotherms for adjustment of their thermal preferenda.

Figure 4. Effect of acclimation temperature on the range of body temperatures selected by Natrix taxispilota in a gradient.



Especially puzzling is the fact that the relationship in Natrix taxispilota is inverse, because the critical thermal maximum is directly correlated with the acclimation temperature (Lowe and Vance, 1955; Larson, 1961; Bradshaw, 1965; Kour and Hutchison, 1970) and PBT, at least in interspecific comparisons, is directly proportional to critical thermal maximum (Brattstrom, 1965; see Fig. 18). These inconsistencies warrant an examination of the ecological significance of the physiological capacity for thermal acclimation in these snakes.

There is some evidence that seasonal acclimation of PBT does occur in temperate zone reptiles. Mueller (1969) found that both PBT (measured in a gradient) and critical thermal maximum were higher in Sceloporus graciosus collected in the summer than in those collected in the spring. Similar increases in the level of field body temperatures from spring to summer have been found in two garter snakes, Thamnophis sirtalis and T. butleri (Carpenter, 1956), and in two lizards, Cnemidophorus sexlineatus and Sceloporus woodi (Bogert, 1949). A similar seasonal variation was found in body temperatures of Natrix taxispilota, but the differences were not consistent with the laboratory evidence for the relationship between acclimation temperature and PBT. The level of body temperature in December and early January ranged between 14 and 20°C and most values were below air temperatures (Fig. 5). By late January, higher air temperatures resulted in body temperatures of 22.5 to 26°C with values approximating air temperature. In March, most body temperatures ranged between 26 and 30°C (Fig. 6) and exceeded air temperature. These observations were made on sunny and relatively windless days when black-bulb temperatures exceeded air temperatures by 4 to 10°C. The occurrence of snake body temperatures below air temperature can be explained only as resulting from recent emergence from cooler water and initial evaporative

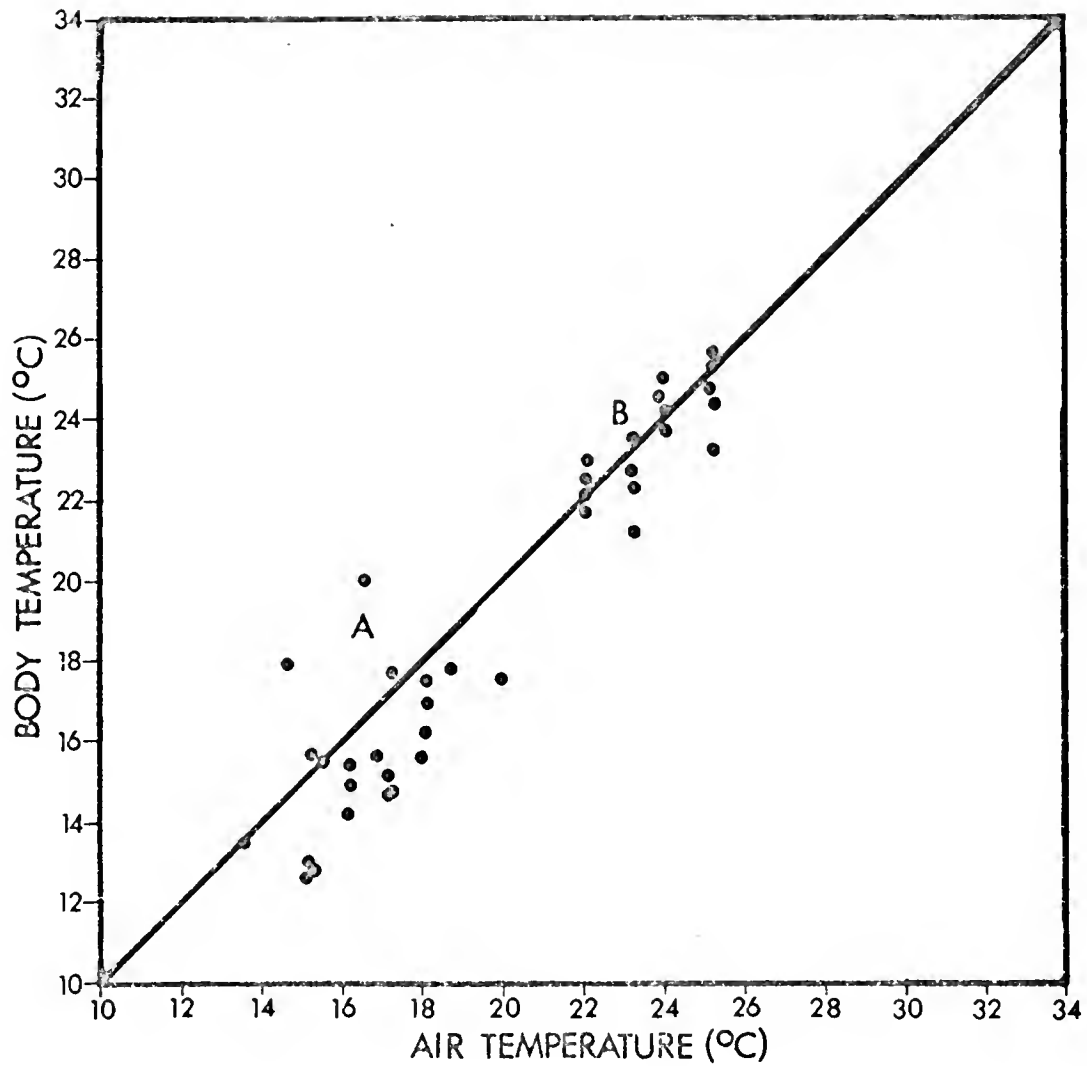


Figure 5. Natrix taxispilota body temperatures and associated air temperatures at Newnan's Lake during (A) late December and early January and (B) late January.

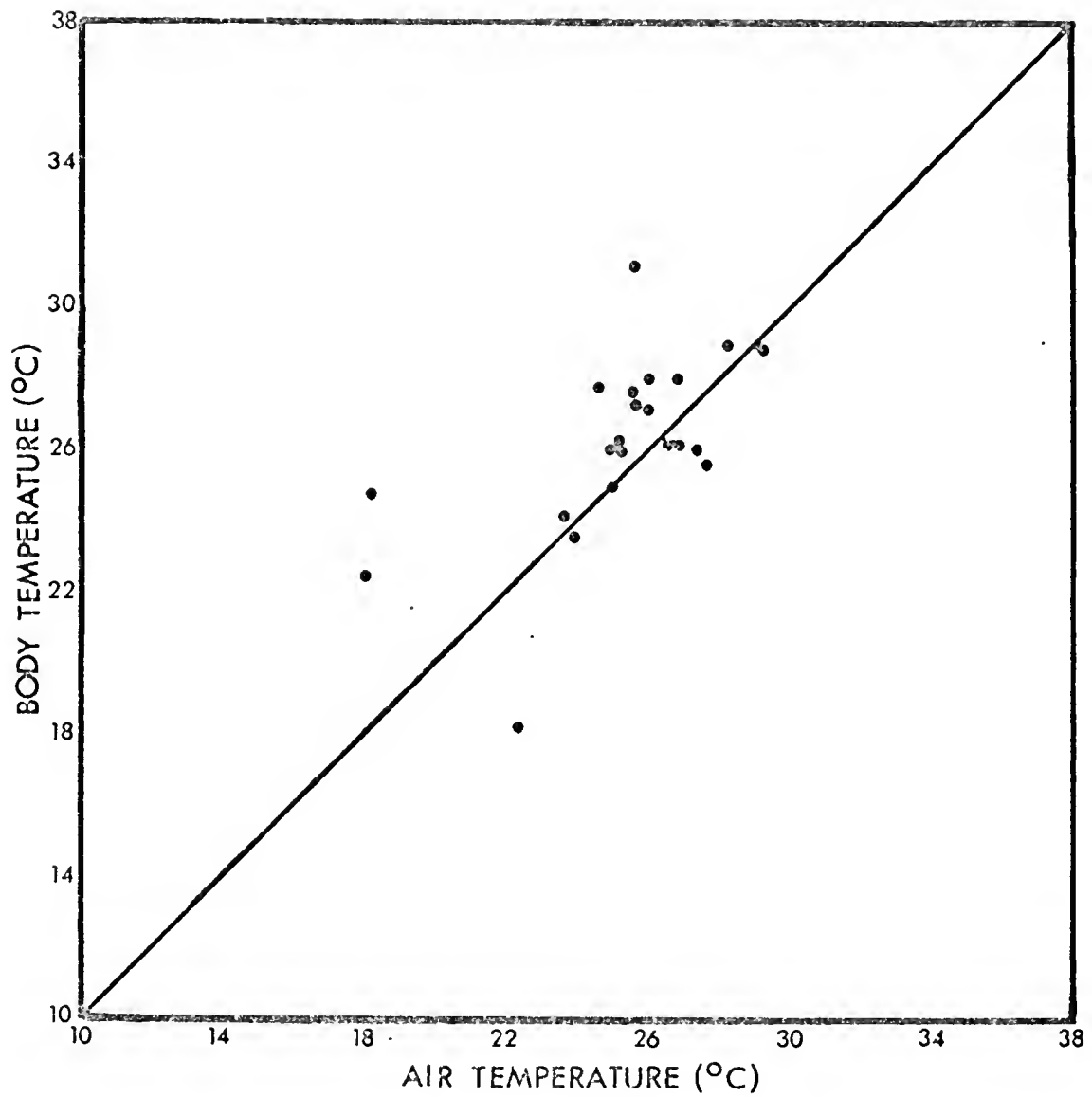


Figure 6. *Natrix taxispilota* body temperatures and associated air temperatures at Newnan's Lake during March.

cooling. Throughout the warmer months, body temperatures remained approximately within the range found in March (Fig. 7), but by mid-October, lower air temperatures again caused a decrease in the field body temperatures. Thus, field data provided no evidence of the inverse relationship that might be expected between seasonal temperature (and presumably thermal acclimation of PBT) and level of body temperature.

However, these field values for winter represent, at best, levels of temperature attainable and not necessarily those preferred. Snakes collected in January selected warmer temperatures in a gradient than those collected in April or July (Table 1), suggesting that acclimation of PBT does occur in nature. The body temperatures selected by snakes collected in April and July did not differ significantly, indicating that these snakes were acclimated to a common thermal level, their PBT. During the colder weather of January, however, thermoregulatory behavior ceased and the snakes became acclimated to the colder thermal regime of the water in which they remained torpid. Their PBT at this time reflected this acclimation.

Metabolic data also suggest this relationship. Figure 8 gives the metabolic rate of snakes as a function of size and acclimation temperature. The level of metabolism at a given temperature is inversely correlated with acclimation temperature. This relationship has been reported for fish, amphibians, reptiles and many invertebrates (for extensive reviews, see Berg, 1953; Bullock, 1955; Fry, 1958) and appears to be a nearly universal characteristic of poikilotherms. When snakes were maintained at varying thermal regimes (30°C from 0901 hours through 2100 hours, 20°C from 2101 hours through 0900 hours), however, their metabolism became acclimated to the higher of the two temperatures (Fig. 8). Acclimation to the highest of varying temperatures has been

Figure 7. Body temperatures of Natrix taxispilota collected at Newman's Lake between 1130-1600 hours from March through October.

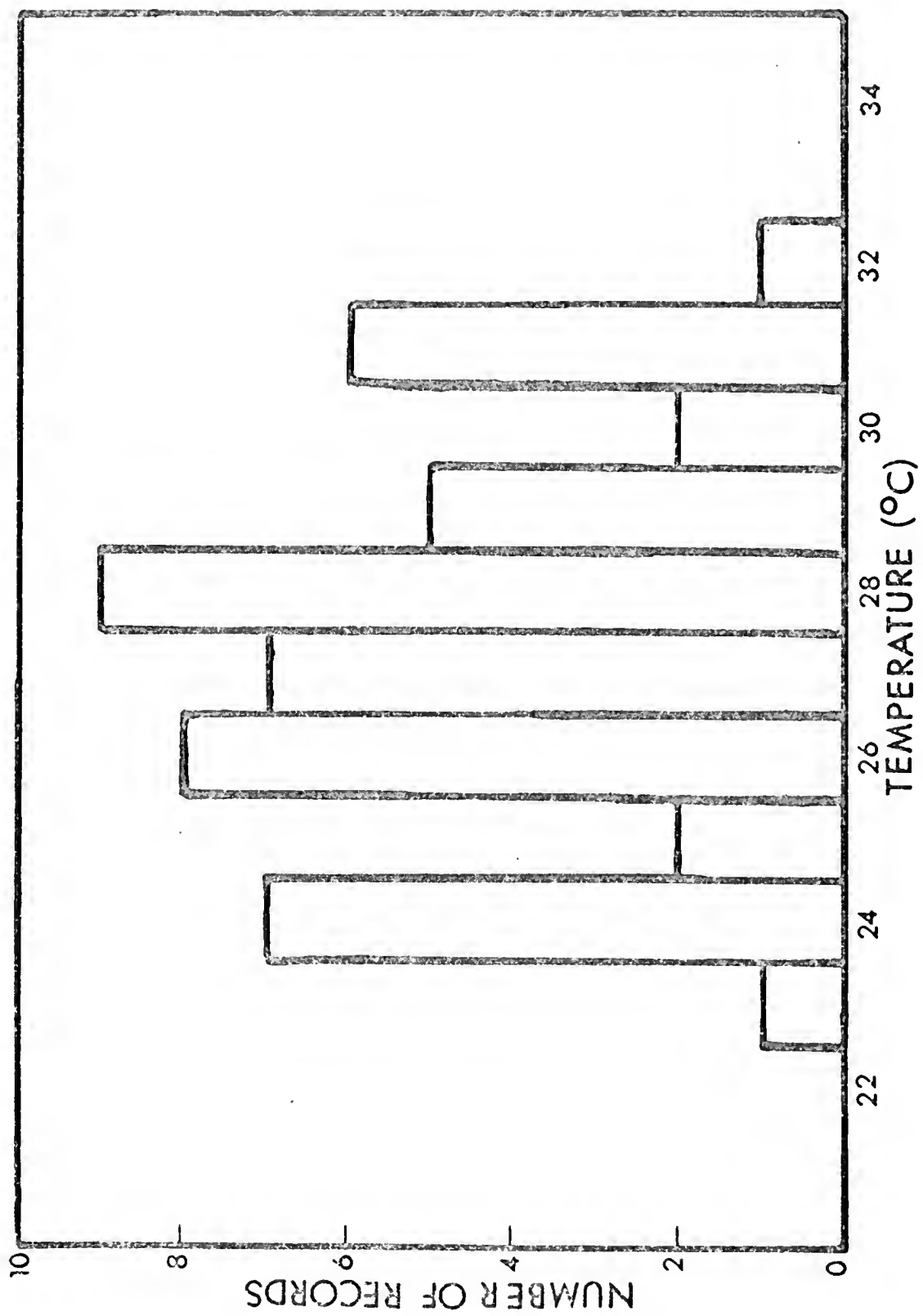


Table 1. The preferred ranges of body temperature of freshly caught Natrix taxispilota.

	JANUARY	APRIL	JULY
PBT RANGE (°C)	29.4-33.5	25.3-30.9	25.2-31.1
MEAN	31.6*	27.9	28.2
N (OBS.)	3 (37)	3 (38)	4 (47)

*Differences between means for April and July are not statistically significant but the mean for January differs significantly ($p=0.05$) from the other means.

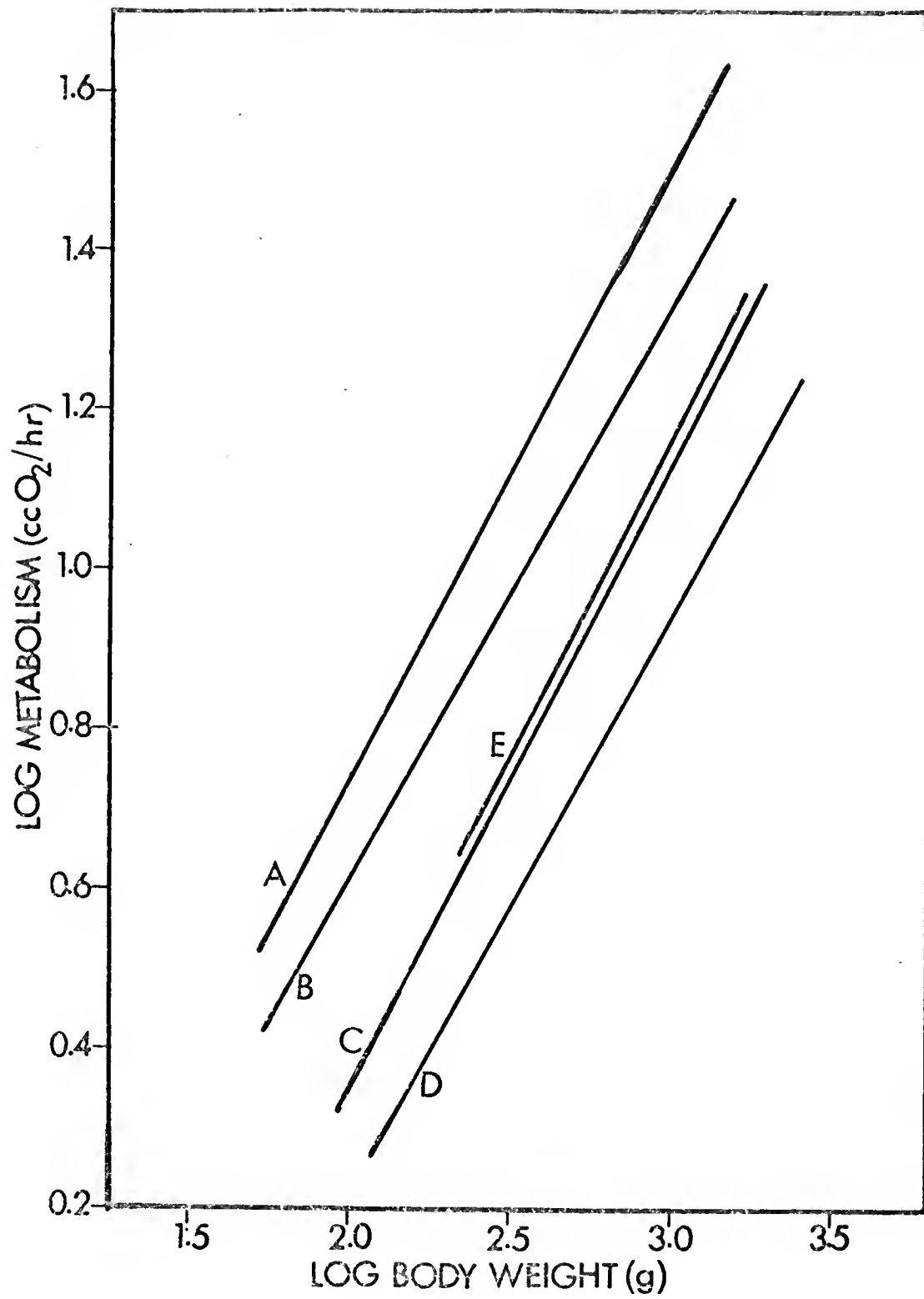
reported for Rana pipiens (Hutchison and Ferrance, 1970) and for several species of fish in both the field (Brett, 1944) and under controlled conditions (Fry et al., 1946; Heath, 1963). These data suggest that a poikilothermal animal can acclimate the level of its metabolism by thermoregulatory behavior. Only when the environmental temperature becomes too cold to permit thermoregulation at the preferred level would there occur acclimation of body functions to a non-PBT level.

There is, then, a seasonal variation in PBT of Natrix taxispilota. It appears that the level at which body temperature is maintained sets the acclimation temperature, and the level of thermal acclimation in turn affects the PBT. The range of body temperatures found in Natrix taxispilota during March through October (23-32°C) correlates almost exactly with those preferred (23.9-33.1°C) by snakes acclimated to 25°C and 30°C -- a close agreement between field and laboratory data. Thermoregulation at the preferred level apparently fixes the level of thermal acclimation throughout those parts of the year when adequate thermal opportunities exist. During the colder months, when this is not possible (Fig. 5), the level of body temperature, and presumably thermal acclimation, varies with water temperature.

The inverse relationship between acclimation temperature and PBT probably represents an overcompensation mechanism which is of value during periods of thermal extremes. It is unlikely that cold-acclimated snakes in nature could ever attain the body temperatures selected by cold-acclimated individuals in a gradient. But by behaviorally thermoregulating in such a manner as to attain these high levels, snakes may significantly elevate their body temperatures. The lower levels preferred by warm-acclimated snakes probably reflect a mechanism that is of importance only in an evolutionary sense. The

Figure 8. Metabolic rate of Natrix taxispilota as a function of acclimation temperature and body weight.

A. acclimated to 20°C, B. 25°C, C. 30°C, D. 35°C, E. varying temperatures (20°C night, 30°C day).



highest air temperature recorded in Gainesville in a 40 year period (Kincer, 1941) is 39.4°C which is several degrees below the probable critical thermal maximum for Natrix taxispilota (Brattstrom, 1965). Only when drastic climatic warming occurs would snakes become acclimated to temperatures significantly above their preferred range and there would be a clear selective pressure favoring individuals who behaviorally sought cool body temperatures even if the lowest attainable body temperature was above the preferred level.

Behavioral Thermoregulation

Morning Emergence

Brown water snakes almost invariably spend the night in the water. The time of emergence depends upon several climatic factors and upon some endogenous responses of the snake.

The effect of air and water temperatures on emergence

Figure 9 shows the response of a 554 g female water snake maintained in the environmental chamber to all combinations of air and water temperatures between 5 and 35°C . This includes all the thermal regimes which the species ever encounters in nature and several artificial situations. The responses of several other animals to a number of these thermal combinations never differed appreciably from those of the 554 g female so the pattern shown in Figure 9 may therefore be considered representative. It should be remembered throughout the discussion that animals used in this laboratory experiment were adapted to the approximate thermal combinations to which their responses were recorded (see Materials and Methods).

The lowest air temperature that elicited emergence was 16°C and then only if the water temperature was 21°C or above. This latter combination is an artificial situation at one extreme of a general

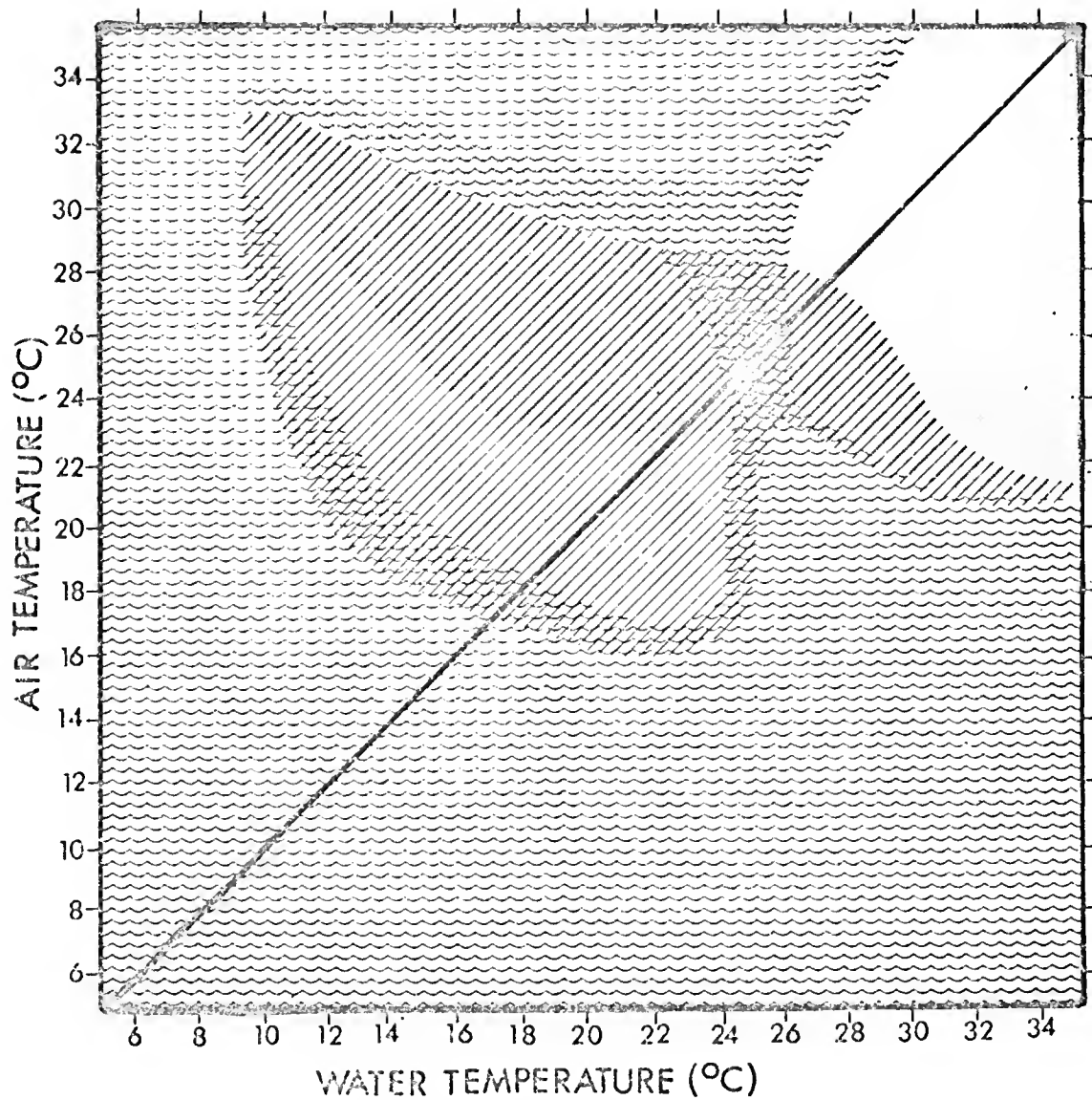





Figure 9. Behavioral responses of a 554 g *Natrix taxispilota* to combinations of air and water temperature from 5°C through 35°C.

-  snake in water
-  snake in sun
-  snake in shade

pattern; the colder the water temperature, the warmer the air temperature needed to elicit emergence. The lowest water temperature at which snakes emerged was 10°C and then only if air temperature was at least 25°C (again an artificial situation). There are, therefore, lower limits for air and water temperatures that elicit emergence in Natrix taxispilota and above these extremes, these minimal values are inversely related. This inverse relationship is not isothermal -- i.e. the slope of this air-water temperature interface is not -1.0.

At a water temperature of 18°C, snakes will emerge for a minimal air temperature of 18°C, but at water temperatures below this level air temperatures must exceed water temperature to evoke emergence (Fig. 9). The lower the water temperature, the greater the air-water temperature differential required for emergence. Values for this differential at or near the water temperature asymptote of 10°C are, as mentioned, not ecologically significant because such differentials do not occur in nature.

At water temperatures above the air-water isothermal emergence point (18°C), the minimal water temperatures that evoked emergence were in excess of air temperature. The higher the water temperature from which a snake emerges, the higher its body temperature at emergence and the less time it takes a basking individual to reach the preferred thermal level. This may explain why snakes emerge from warm water into cooler air at water temperature above 18°C. Although the water is relatively warm, it is still below the preferred level. Basking permits attainment of PBT, or at least a closer approximation than is represented by the water temperature. Thus, snakes apparently will not emerge when their body temperatures are

below 18°C unless the aerial phase insures rapid attainment of this level.

Figure 10 summarizes the field relationship between air and body temperature. It is significant that only 5 percent of the body temperature records are below 18°C , a close agreement with laboratory results. The decrease in number of records for snake body temperature at air temperatures below 18°C is precipitous and not a gradual attenuation. The body-air differentials maintained by snakes at air temperatures from 18°C through 30°C are inversely correlated with air temperature (Fig. 11). This is clearly a reflection of differential utilization of sunlight as a function of environmental temperatures.

It is ecologically significant that there exists a lower thermal threshold for thermophilic responses as evidenced by the refusal of snakes to emerge at water (and therefore body) temperatures below 10°C even when air temperature was warmer. Below the body temperature required for coordinated locomotion, emergent snakes would be very vulnerable to predation by homoiotherms. Also, at temperatures below the thresholds for feeding and digestion, thermophilic responses would increase the metabolic maintenance cost without providing additional energy sources. This would deplete the reptile's energy stores needed for periods of torpor and (at higher latitudes) hibernation.

When the water temperature approached the lower limit of the preferred range (25°C), a common occurrence between April and October, the minimal air temperature required to evoke emergence increased sharply from 17°C at 24°C water temperature to 23°C at 25°C water temperature (Fig. 9). At water temperatures above 25°C , the minimal air temperatures necessary for emergence were inversely proportional

Figure 10. Body temperatures of Natrix taxispilota and associated air temperatures at time of capture at Newnan's Lake.

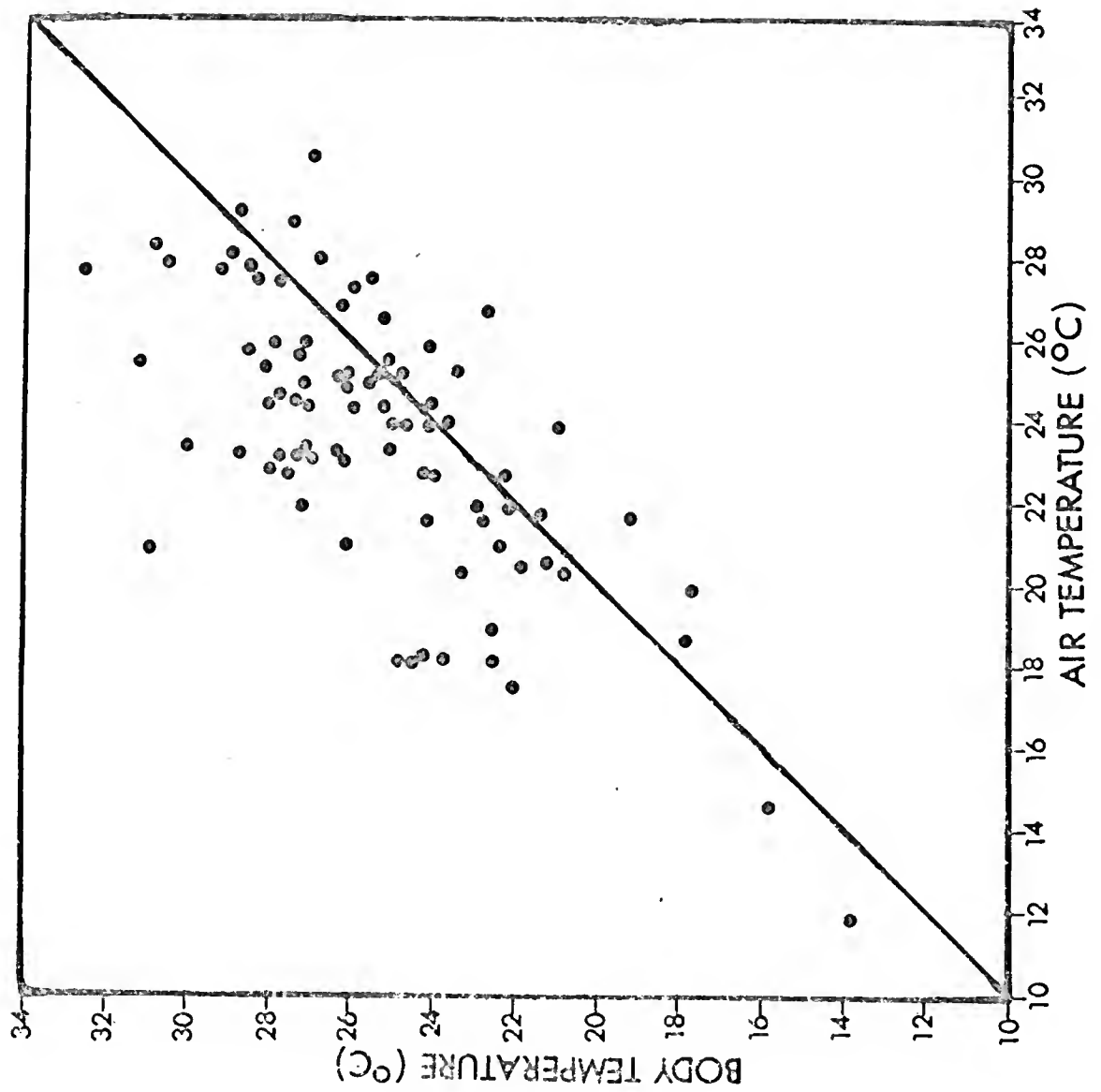
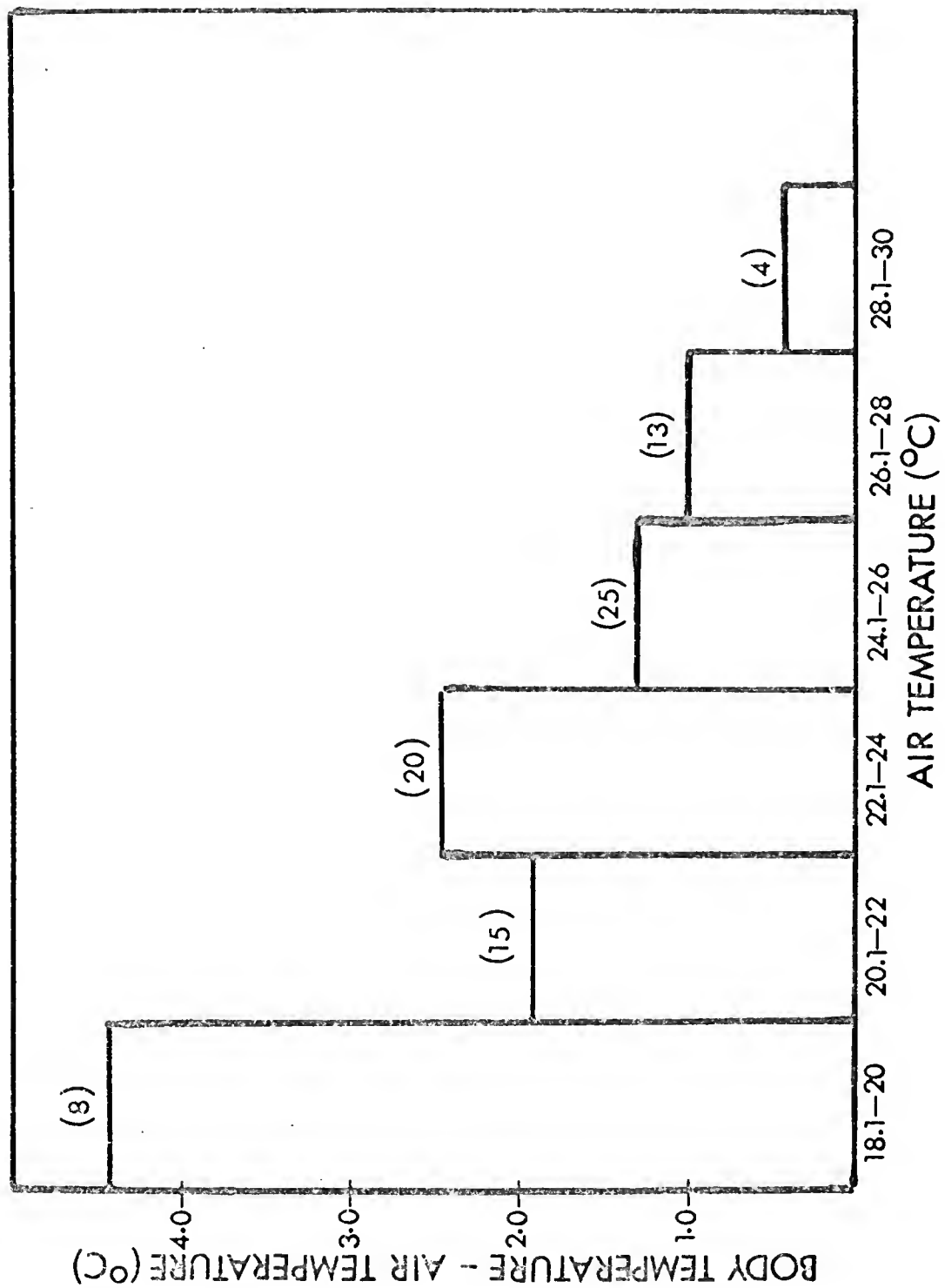


Figure 11. Average body-air temperature differentials of Natrix taxispilota at Newnan's Lake as a function of air temperature. Data are the same as those plotted in Figure 10. Numbers in parentheses indicate number of snakes in each category.

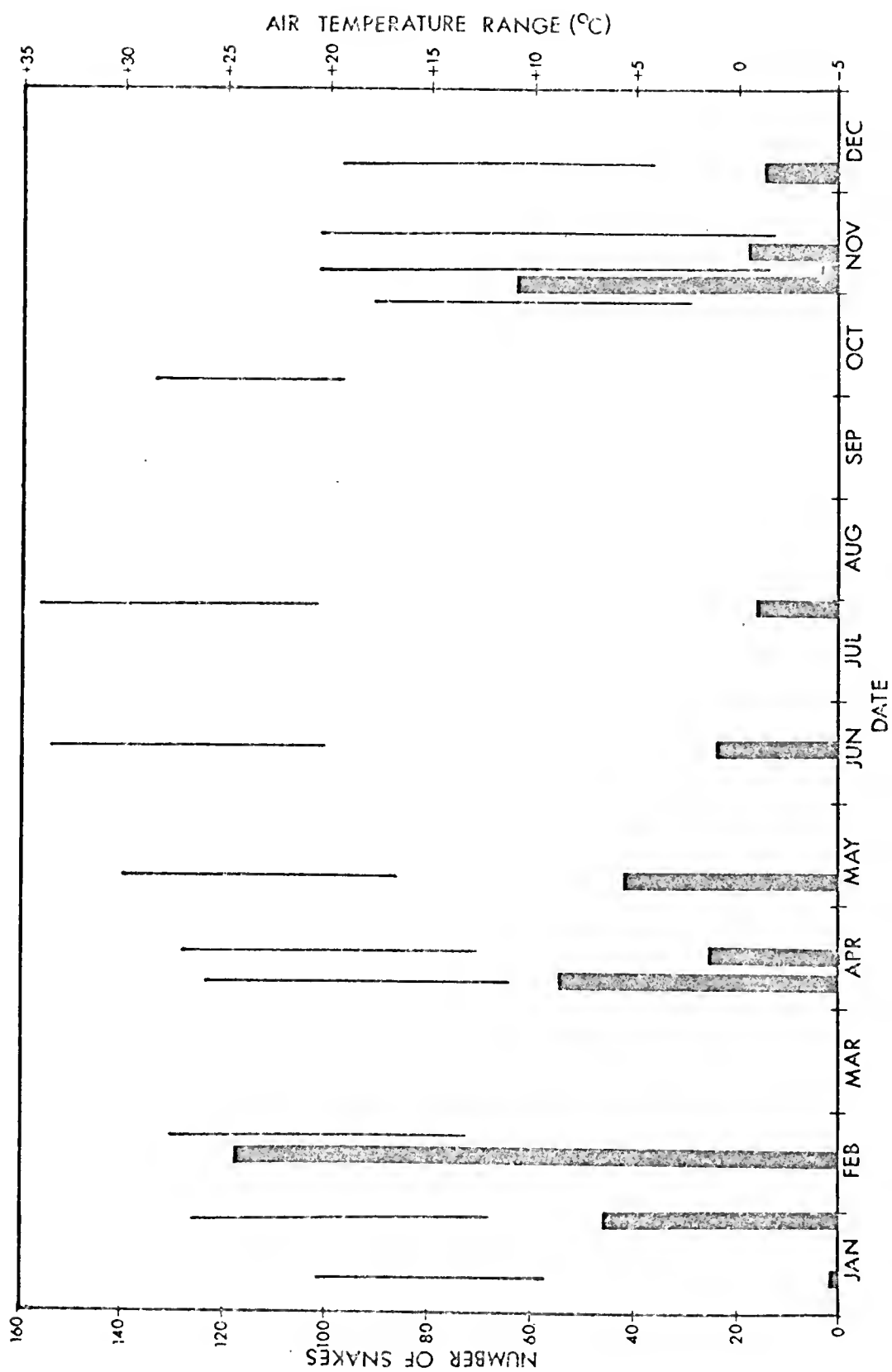


to water temperatures. This sharp increase in the minimal air temperatures necessary to elicit emergence suggests that water is of considerable importance for thermoregulation between April and October when such thermal conditions are common. When water temperatures exceeded the PBT, emergence into lower air temperatures permitted cooling to the preferred level. These water-air temperature differentials probably never obtain in nature, and ordinarily, water temperatures appreciably above air temperature would occur in the evening well after the emergence period.

The effect of acclimation on emergence

Animals used in the environmental room studies were adapted to the air-water temperature combinations to which their responses are graphed in Fig. 9. In the wild, this is not always the case. Sudden climatic changes may result in exposure of snakes to a thermal environment to which they are not physiologically adapted. For instance, the same approximate air and water temperature ranges on February 20, 1971 and April 16, 1970 resulted in the emergence of 118 and 25 snakes respectively (Fig. 12). Both days were relatively humid and windless so the disparity seems to be a reflection of the difference in climatic conditions during the week preceeding these dates. April 16 was warm and typical of the weather of this period, and snakes were physiologically acclimated to their PBT. February 20, however, was the warmest day of a four day warming trend. Night air temperatures had been at or near freezing until February 18. These snakes, then, were acclimated to temperatures well below those of February 20 and the basking response was greatly accentuated. These data and the relationship between acclimation temperature and PBT suggest that the minimal air and water temperature combinations required to elicit emergence and basking are lower in cold than in warm-acclimated snakes.

Figure 12. Number of Natrix taxispilota (bars) basking at Newnan's Lake on various days throughout the year (summation of data from 1969, 1970 and 1971) and the ranges of air temperature (vertical lines) recorded at the Gainesville weather station for those days.



Effect of physiological state upon emergence

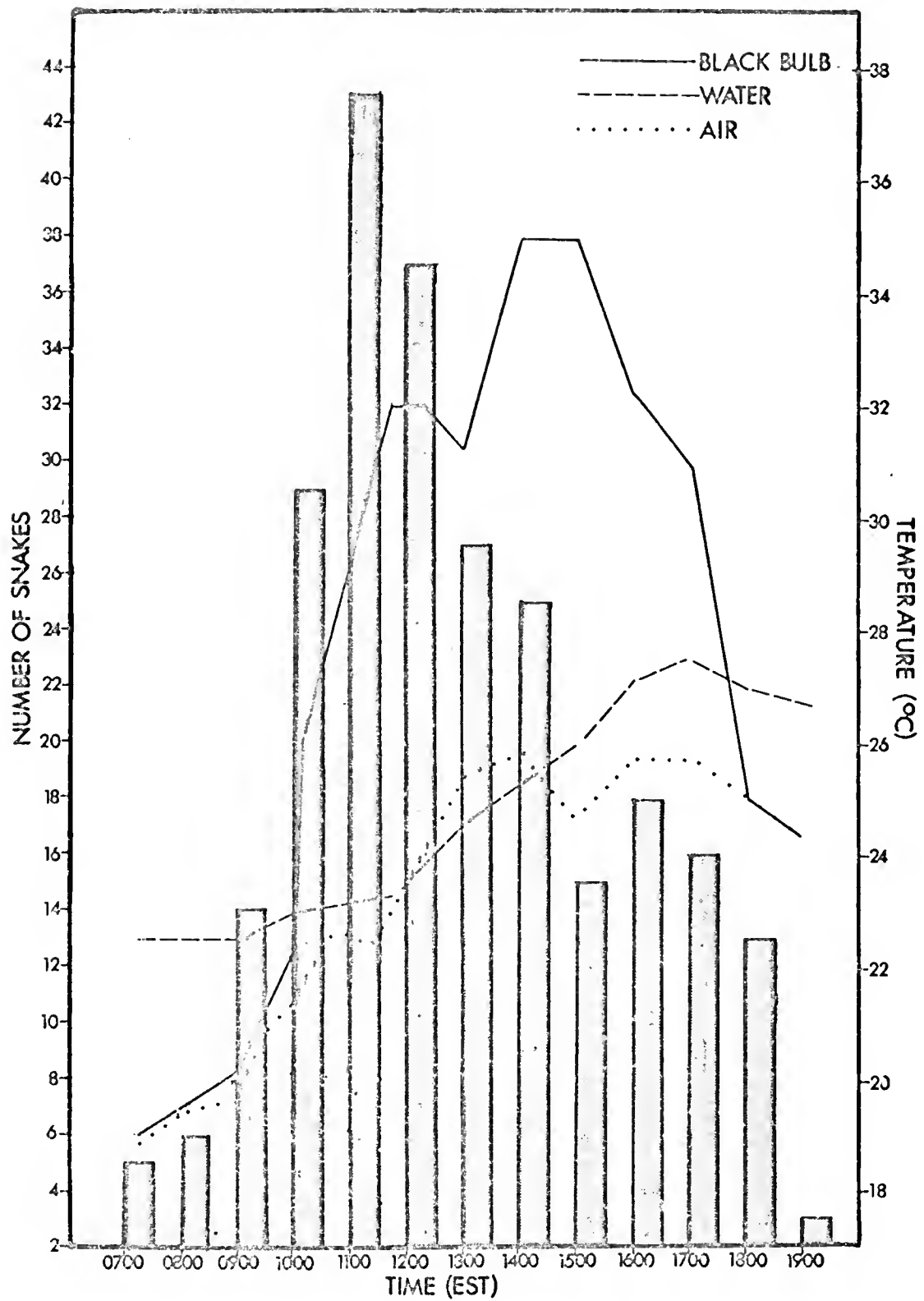
At 0920 on April 1, 1967, a snake was found basking with a body temperature of 13.8°C . Corresponding air and water temperatures at the time were 11.9°C and 13.8°C respectively. These were the lowest body temperature and associated environmental temperatures recorded during this study (Fig. 10). It is probably significant that this individual had a prominent bulge from a fish it had recently eaten. It is possible that the minimum air and water temperatures necessary to evoke basking may be lower in snakes digesting food than in those in a postabsorptive state. Presumably, higher body temperatures should facilitate digestive processes in reptiles (Cowles and Bogert, 1944; Regal, 1966).

Effect of light on emergence

Combinations of air and water temperatures ideal for basking did not induce emergence at any hour in the absence of light. When the sun lamp was turned on during the night, snakes basked if thermal conditions were proper. Boyer (1965) found that turtles also would bask in response to light at any time. During cloudy weather, basking behavior was either diminished (i.e. fewer individuals emerged) or emergence was delayed. Boyer, (1965) found this also to be true for turtles. In the semiaquatic reptiles studied, therefore, basking behavior does not appear to be an endogenous rhythm, but a response to the proper conditions of light, water temperature, and air temperature. The physiological state of the animal is an important factor in determining the level of the environmental temperatures necessary to induce emergence.

Figure 13 presents the thermal environment at Newnan's Lake on April 9, 1970 and the emergence response of snakes. Climatic conditions

Figure 13. The number of Natrix taxispilota basking at Newnan's Lake at various times on April 9, 1970, and the associated air, water, and black bulb temperatures.



on this day were typical of the preceding week so these animals were adapted to this general thermal regime. The water temperature exceeded air temperature until 1200 hours but a peak in basking activity occurred earlier. Emergence appeared to be initially triggered by the onset of lighting, and to be accentuated by the rise in black-bulb temperature.

Temporal changes in emergence response following initial onset of light

On many days, the initial air-water temperature combination used was below the emergence threshold. Every two hours, air temperature was raised 2°C and responses were recorded. Under such conditions, there occurred a temporal change in the snakes' propensity for emergence. Temperature combinations which would elicit emergence before about 1500 hours (EST) could not elicit initial emergence after that time. The responses recorded in Fig. 9 were all recorded prior to 1500 hours. The heating rate ($\Delta T_{\text{air}} = 2^{\circ}\text{C/hr}$) and general warming pattern approximate conditions occurring in the wild during winter. Under laboratory conditions, 1500 hours occurred halfway through the "sunlight" cycle (0900-2100 hours). In nature, six hours after sunrise would be about 1300 hours EST during December and January. An animal initially emerging after this time in response to threshold emergence temperatures would begin to thermoregulate at or following the peak air temperature of the day and would confront decreasing (and therefore sub-threshold) air temperatures for the remainder of the day. Clearly, then, this temporal restraint on the thermophilic emergence response is necessary to restrict thermoregulatory activity to thermally hospitable periods. Otherwise, extensive basking would occur at low body temperatures resulting in exposure of snakes to predation at suboptimal activity temperatures.

Maintenance of Preferred Body Temperature

Elaborate behavioral adjustments permit some lizards to thermoregulate within very narrow limits. Desert lizards apparently have the most elaborate behavioral repertoire, including postural adjustments (Bogert, 1949; Norris, 1953; Heath, 1965), retreat to burrows (Cowles and Bogert, 1944; Norris, 1953; DeWitt, 1967a, 1967b; McGinnis, 1967), panting (Cole, 1943; Cowles and Bogert, 1944; Ruibal, 1961; Kour and Hutchison, 1970), climbing (Norris, 1953; DeWitt, 1967a) and burrowing (Cowles and Bogert, 1944; Heath, 1965). Physiological modifications are known in these reptiles, but are clearly of secondary importance in thermal homeostasis. Thermoregulation in snakes has been studied very little and available information suggests that thermal control is not as precise, and the behavioral repertoire not as complex, as in the case of heliothermic lizards.

Following emergence, brown water snakes basked under the sunlamp (or lay in the shade at higher air temperatures) until a body temperature in the preferred range was reached and thereafter moved from the "sun," to shade, to water in order to maintain this level. No consistent postural or coiling adjustments were noted. Retreat to the shade or entrance into "sunlight" usually required 5 to 15 minutes. This slow pace is probably the result of a slow heating and cooling rate to be expected in an animal of such bulk and the wide range of preferred temperatures.

At water temperatures below 25°C (and appropriate air temperatures), snakes emerged and basked in the "sunlight" until their PBT was reached and then moved into the shade. There is a broad zone of overlap between air temperature at which animals basked in the "sun" and those at which they retreated to the shade. This appears to be largely a

reflection of the distance between the snake and the sunlamp; the ecologic equivalent would be the directness and/or intensity of sunlight. Similarly, there was overlap between the air temperatures at which animals lay in the shade and those at which they entered the water. This probably is a reflection of variation in body temperature of the snake, from one experimental run to the next, at the time it retreated from the "sunlight."

The lowest air temperature at which snakes retreated to shade was inversely proportional to water temperature at water temperatures from 10°C through 18°C. Evidently, more time was required at these low water temperatures (emergence body temperatures) for attainment of preferred levels. This resulted in the recorded extreme of a snake basking in the "sun" at an air temperature of 31°C following emergence from 10°C water.

In one air-water thermal regime, snakes could be found in either air, water, or "sun" (Fig. 9). This was between water temperatures of approximately 23°C and 27°C and air temperatures of 23°C and 28°C. These are evidently the only water temperatures above 10°C at which snakes may not emerge at all. At water temperatures above this zone, there is a decline in the realm of air temperatures at which emergent snakes bask in the sun, a marked increase in the shade realm, and an extinction of the shade-sun overlap zone. When air and water temperatures exceeded the preferred level, snakes lay in the shade. These temperature combinations rarely or never occur in nature and the value of such behavior is not clear.

In nature, extensive movement among the shade, sunlight, and water usually occurs only in the late fall, winter, and early spring. Low ambient temperatures at these times necessitate such thermoregulatory behavior and the sparseness of foliage permits abundant

access to sunlight. At such times (Fig. 13) the number of individuals basking usually peaks in late morning and declines thereafter. There is an individual turnover and during the afternoon, submergence rate exceeds emergence rate resulting in a decrease in the number of basking individuals. The first individuals to attain PBT and eventually reenter the water are probably the smaller animals since they heat more rapidly. Data taken on March 5 substantiate this (Fig. 14). Between 1100 and 1300 hours, there was an inverse relationship between size of basking individuals and the body-air temperature differential. No such correlation existed between 0900 and 1100 hours, indicating that time of emergence was independent of body size. Figure 15 shows the changes in body temperature of a Natrix taxispilota, and the associated environmental temperatures under natural climatic conditions of November 28, 1970, at Lake Alice.

During the warmer months (mid-April through mid-October), such thermoregulatory behavior is seldom necessary, because air and water temperatures during the day are usually within the PBT of this species. Because of the level and wide range in PBT, snakes occasionally were found to bask in one location from time of emergence until evening submergence. Water temperatures during these months were often within the preferred range, and most snakes either remained in the water or had submerged by census time (Fig. 12).

Evening Submergence

With the approach of nightfall, few if any snakes remain on basking sites above the water (Fig. 13). In initial laboratory experiments, where lights came on at 0900 hours and went off at 2100 hours, snakes usually emerged within an hour of onset of lighting (given proper thermal conditions) and submerged within the 30-minute period after

Figure 14. The relationship between body size and body-air temperature differentials of Natrix taxispilota collected between 1100 and 1300 hours on March 5, 1967.

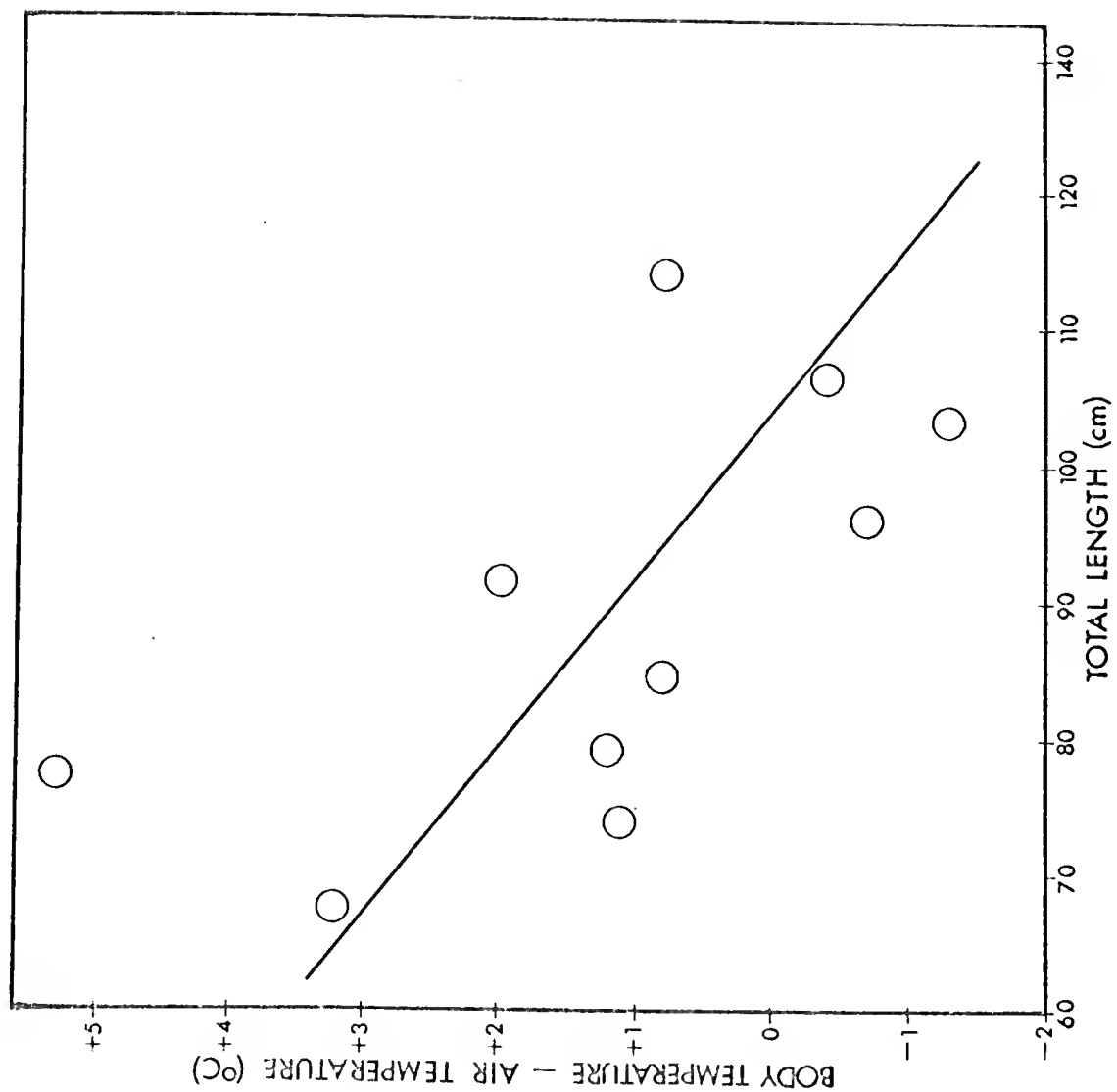
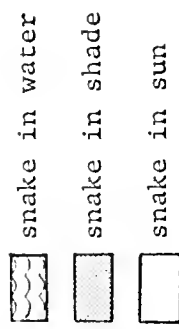
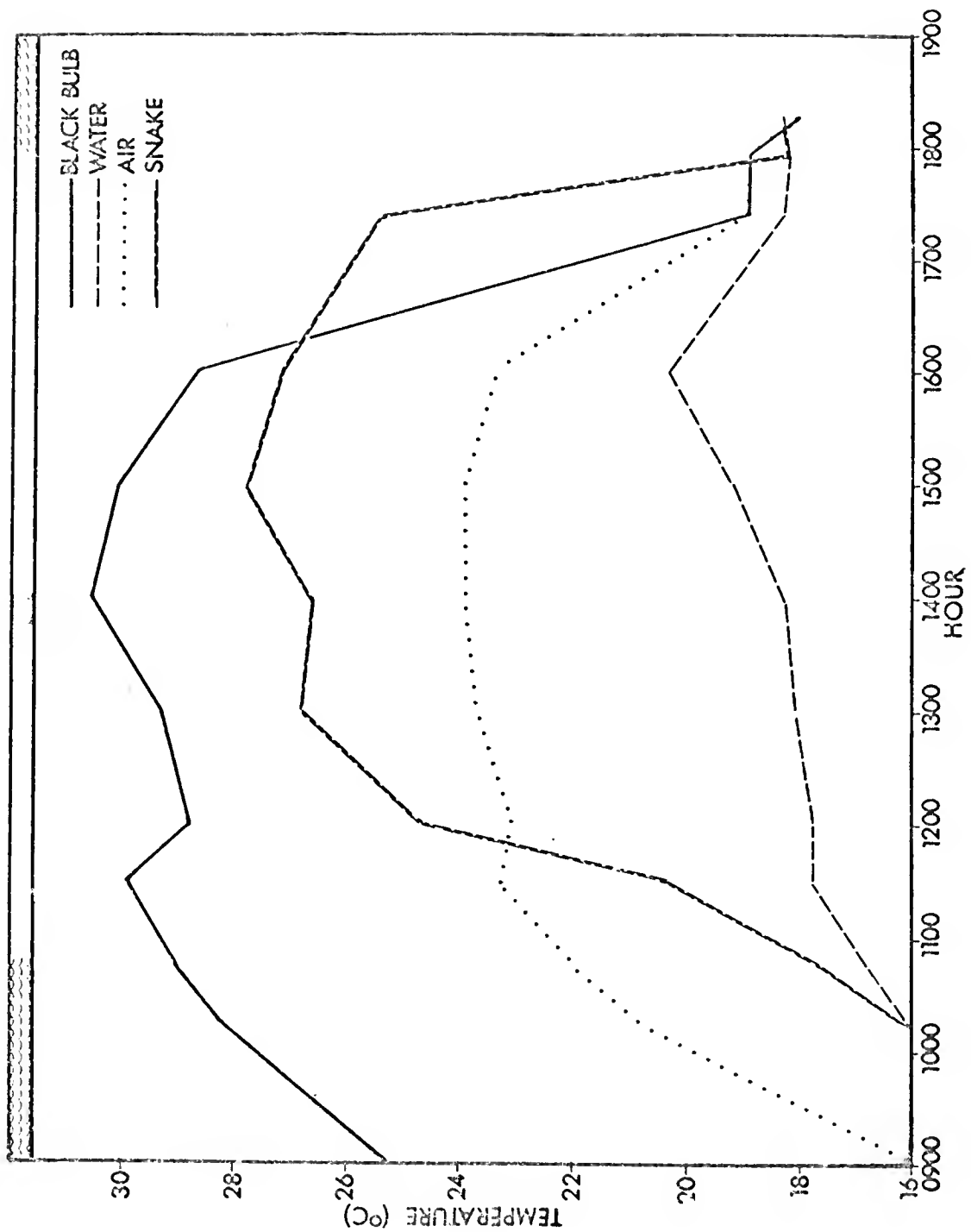


Figure 15. Changes in body temperature of a Natrix taxispilota thermoregulating under natural climatic conditions of November 28, 1970, in experimental pen at Lake Alice.





light was terminated. After several weeks exposure to this photoperiod, however, snakes often entered the water an hour or more before 2100 hours.

This evening submergence appears to be a temperature-independent response to decreased light; snakes slide into the water regardless of the air-water temperature differential. Boyer (1965) noted that most basking turtles left their basking sites and submerged prior to 30 minutes before sunset, although no mention was made of air and water temperatures at these times. Since evening submergence is evidently common in most semiaquatic reptiles, and since it is temperature-independent (at least in Natrix taxispilota), this response probably represents a predator avoidance behavior. Clearly much feeding -- almost exclusively on fish -- does occur at this time, when water temperatures permit; but little feeding behavior probably occurs below a water temperature (and therefore body temperature) of 15°C (Lueth, 1941). Large fish could ingest small Natrix, but only alligators would represent a substantial predation threat to brown water snakes during the aquatic phase of their activity cycle.

In natural situations, the water is usually warmer at night ~~than~~ ~~than the air~~. It may be, therefore, that evening submergence evolved as a thermal response and persists even in the unnatural situations to which snakes were subjected in the laboratory.

Factors Affecting Preferred Body Temperature

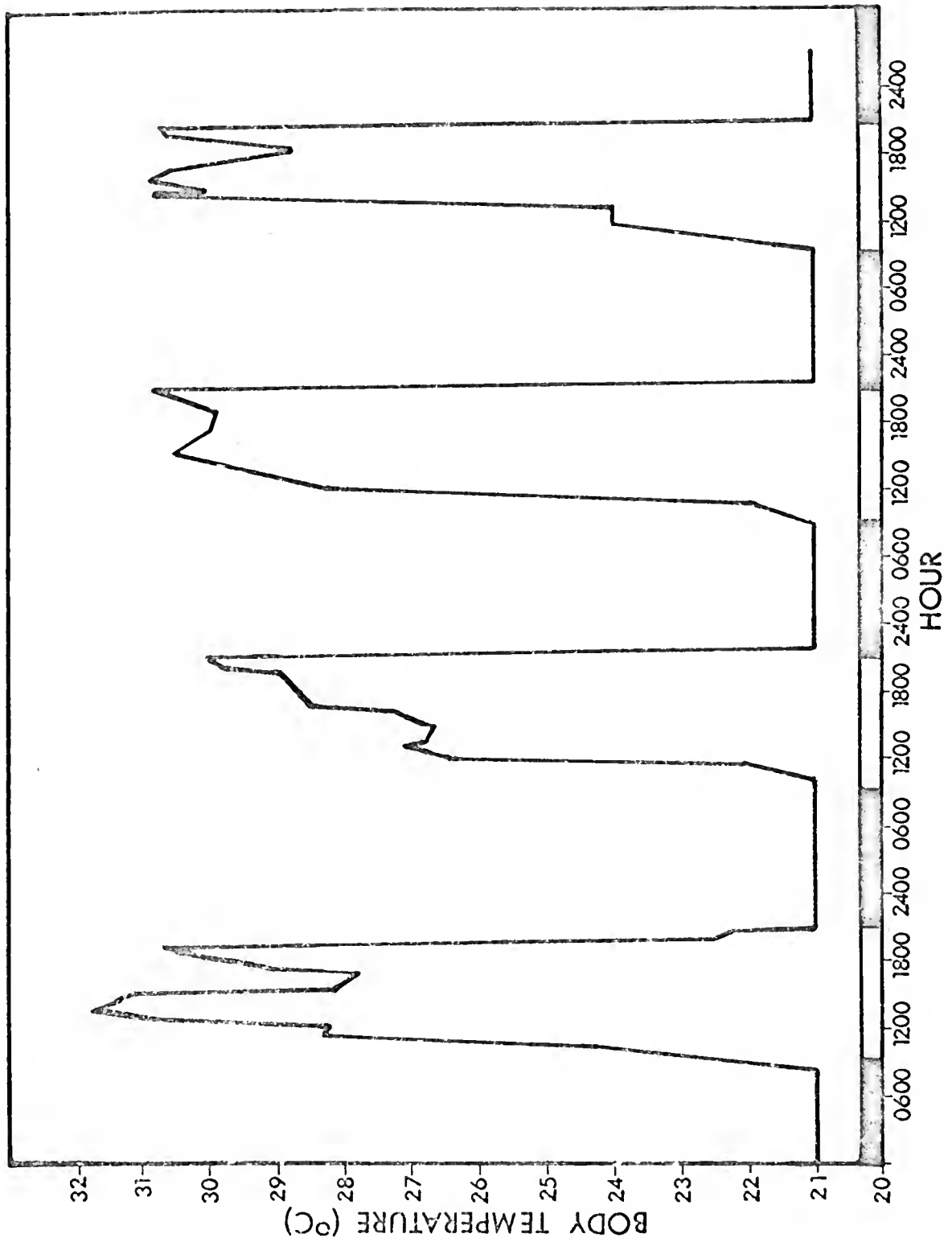
As previously mentioned, there appears to be a mutually causal relationship between the level of physiological acclimation and PBT, resulting in a fixed preferred level of about 25-30°C throughout most of the year. There are other ecologically relevant factors which may alter the level of preferred temperature, at least temporarily.

Digestion

Snakes acclimated to 25°C were fed fish containing ingestible transmitters and were found to regulate (in a gradient) at a warmer end of the normal range (Table 2). The same pattern was found in animals that were given access to a heat lamp in an isothermal (21.0°C) environment. Two Natrix taxispilota were fed fish containing transmitters and permitted to thermoregulate in this environmental chamber. The level of air and water temperatures was low enough to induce basking but high enough to permit attainment of body temperatures in excess of 30°C by basking under the sunlamp. The first day following feeding, these snakes spent at least half the day in the water before emergence. This delayed emergence is probably unrelated to thermoregulatory behavior. It is a common behavioral trait of captive snakes, including terrestrial species, to submerge in any available water after consuming a large meal. The moisture evidently facilitates stretching of the skin, or at least provides better support for the portion of the body containing the food. Upon emergence, snakes maintained body temperatures mostly between 27.5°C and 31°C. When they first emerged, the snakes usually lay with the bolus directly under the sunlamp and moved to a cooler area after body temperature reached 30°C to 32°C. A four-day thermal record for one of these snakes is shown in Fig. 16.

Thermophilic responses to feeding have been reported for other reptiles (Regal, 1966; Bustard, 1967; Kitchell, 1969) including two semiaquatic snakes, Natrix sipedon and Thamnophis sirtalis. In all cases, the preferred thermal range following feeding seems to constitute a sub-range of the postabsorptive PBT. This increase in precision of thermoregulation has in all cases been interpreted as a facilitation of digestive processes.

Figure 16. Four-day body temperature record of a Natrix taxispilota digesting a fish eaten on March 23, 1971. Throughout the first day of digestion, the snake remained in the water (see text); the subsequent four-day period is shown. Air and water temperature were maintained at 21°C. Dark bars indicate periods of darkness; light bars indicate periods of light.



The effect of temperature on digestive efficiency was determined for Natrix taxispilota at 20, 25, 30, and 35°C. The greatest extraction efficiency occurred at 30°C (Fig. 17) and decreased both above and below this temperature. This thermal level corresponds to the preferred level for digestion (Table II). Regurgitation of food was very common among snakes maintained at 35°C, another indication that this was supraoptimal thermal level for digestion. Below 30°C, digestive efficiency decreased with decreasing temperature but the 82.6 percent efficiency level at 20°C is still a substantial figure. It is obvious that high body temperatures expedited digestion but were not absolutely necessary, indicating that under natural conditions, digestive processes would continue at night well after submergence if water temperature was not excessively cold. This wide range of digestive activity is probably necessary in such poikilotherms to prevent putrefaction of ingested food at night and during other periods when body temperature falls well below 30°C. Putrefaction would be a particularly great problem in snakes since they ingest items whole and the internal tissue of ingested items would not be reached by gastric enzymes for many hours or days if digestion ceased at temperatures slightly below the optimal level.

The influence of temperature on gastric digestion in the European grass snake, Natrix natrix, was studied by Skoczylas (1970) who used x-ray photography to determine the speed of digestion at temperatures of 5, 15, 25, and 35°C. He found that digestion was completely arrested at 5°C and proceeded very slowly (or ended in regurgitation) at 15°C. Digestion was complete at both 25 and 35°C but was faster at 25°C. Digestive rates in the king snake, Lampropeltis getulus, were found by Root (1961) to be similar to those of N. natrix below

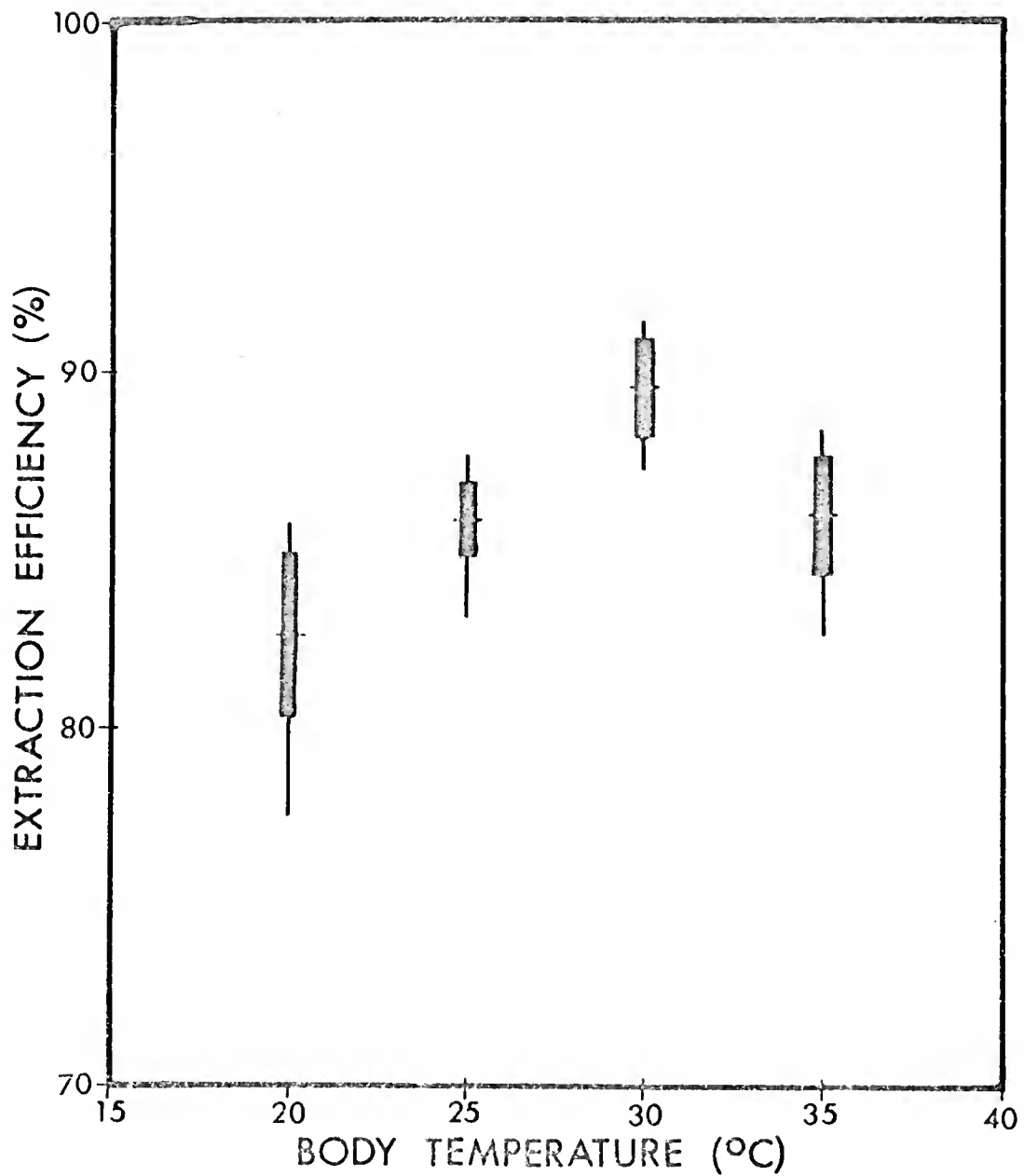


Figure 17. The effect of temperature on digestive extraction efficiency of *Natrix taxispilota*. Horizontal line, mean; vertical bar, standard deviation; vertical line, range.

Table 2. Effect of digestion on the normal range of preferred body temperatures.

	POSTABSORPTIVE	DIGESTING
PBT RANGE ($^{\circ}\text{C}$)	25.7 - 32.6	28.2-32.1
MEAN	29.86	30.28
N (OBS.)	5 (66)	4 (49)

25°C, but the maximum digestive rate occurred at the highest temperature employed, 33°C. Skoczylas attributed the discrepancy in digestive rates of the two species at 33-35°C to intraspecific differences in PBT.

Research on digestive rates of other poikilotherms tends to substantiate this generalization. Many freshwater fish are able to digest food at 2°C to 5°C (Wangensteen et al., 1958; Molnar and Tölg, 1962). These temperatures are below the lower limit of the thermal activity range of Sphenodon punctatus, the lowest known for any reptile (Bogert, 1953a, 1953b). In fish studied over a wide range, digestive rate appears to be directly correlated with water temperature (Riddle, 1909). However, the rate of food input may also influence digestive efficiency. Davies (1964) found that in Carassius auratus, the proper level of food input could increase extraction efficiency to 92-94 percent at either 21.5°C or 12°C. Other workers (Ivlev, 1939; Gerking, 1955) have found extraction efficiencies of other fish at a given temperature to be independent of input rate. Amphibians also show wide thermal ranges for digestion (Pegel, 1939; Joly, 1958; Root, 1961) and are capable of digesting at temperatures less than 10°C, levels at which peristalsis ceases in most reptiles (Skoczylas, 1970). The processes of gastric digestion and peristalsis may have different thermal thresholds, as in the painted turtle, Chrysemys picta, which cannot digest, but maintains peristalsis, at 5°C (Fox and Masacchia, 1959). Nonheliothermic poikilotherms, therefore, seem to have lower thermal thresholds for digestive processes than heliothermic species.

Other Factors Affecting Preferred Body Temperature

Regal (1967) clearly demonstrated that several species of lizards placed in a gradient will select night temperatures that are well below their preferred diurnal PBT. This was true of Klauberina riversiana,

a nocturnally-active lizard, as well as three heliothermic diurnally-active forms. No such endogenous variation in the level of PBT was found in Natrix taxispilota maintained in a gradient. From April through October, water temperatures at the study site were generally warmer at night than air temperatures. A voluntary hypothermic response to darkness would therefore be inconsistent with their behavior. Evening submergence appeared to be a temperature-independent response to diminished light.

The data of Kitchell (1969) suggest that snakes undergoing ecdysis actively select body temperatures below their normal PBT. The three species he investigated included two semiaquatic species, Thamnophis sirtalis and Natrix sipedon. The latter, when not shedding, had a PBT of $28.03 \pm .28^{\circ}\text{C}$ (mean \pm standard deviation) but a preference of $18.71 \pm .38^{\circ}\text{C}$ when undergoing ecdysis. In the present study, there were not enough data available to detect such voluntary hypothermic response to ecdysis but, in view of the unanimity of Kitchell's data for three species of snakes -- one congeneric with N. taxispilota -- it seems likely that brown water snakes have lower thermal preferenda when shedding.

No pregnant females were used in this study but data from several sources suggest that such individuals have thermal preferences that differ from those of males and non-pregnant females. Stewart (1965) found in Thamnophis sirtalis and T. ordinoides "a consistent tendency for pregnant females of both species to maintain relatively high body temperatures." Fitch (1960) found that gravid female copperheads, Ancistrodon contortrix, regulated within more precise limits than males or non-pregnant females and noted that "most of the copperheads found basking in sunshine in summer were females." Osgood (1970) found

pregnant female Natrix taxispilota and N. fasciata to thermoregulate within a narrower temperature range than males or non-pregnant females, but his sample for Natrix taxispilota consisted of only four individuals (three pregnant females, one male). In all of these accounts, the body temperatures fell within the limits of the normal PBT but constituted a smaller sub-range within it.

The effect of intraspecific differences in size upon PBT has been examined by several workers, inter alia Bogert (1949), Wilhoft (1958), Hirth (1963), and Brooks (1968). Only in Basiliscus vittatus (Hirth, 1963) were statistically significant differences found and the differences were so slight ($35.3 \pm 0.05^{\circ}\text{C}$ in juveniles, $34.7 \pm 0.07^{\circ}\text{C}$ in adults) that ecological significance cannot be ascribed. The most likely candidate for an ecologically significant change in PBT with size is probably Varanus kemodoensis, the world's largest lizard. This species is arboreal as a juvenile and becomes terrestrial upon attaining the length of 1.5 to 2.0 meters (Walter Auffenberg, private communication). It would be surprising if a change in PBT did not accompany this change in habitat preference.

The PBT in a given species of reptile, then, is not an immutable thermal level. It may undergo temporal changes and changes reflecting the thermal optima for various physiological processes. It has long been known that snakes undergoing ecdysic processes refuse to feed. This behavior pattern has been interpreted as a response to avoid damage to the newly developing epidermal layer which would be severely stretched or even split by the ingestion of large items. The preceding discussion of the thermal requirements of these two processes (ecdysis and digestion) in reptiles, suggests a thermal incompatibility and certainly presents at least as strong an argument for their non-concurrence.

The Ecological Significance of Reptilian Preferred Body Temperature

Many workers (Ruibal, 1961; Brattstrom, 1965; Kitchell, 1969; Skoczylas, 1970) have commented on the empirical relationship between the PBT of reptiles and the microclimate of their habitat. Again, these generalizations deal mostly with lizards. Diurnally-active desert lizards generally have higher PBTs than lizards from non-desert areas. Diurnal reptiles generally have higher thermal preferenda than nocturnal species. Surprisingly, the significance of this relationship has never been examined from the standpoint of causality. Existing data on reptilian thermal preferences and tolerances suggest that climate may be a major factor in evolutionarily setting the level of PBT.

The thermal extremes between which reptiles must live are the approximate levels that freeze their tissues and those that denature their proteins, or in other ways cause physiological heat-death. But most, if not all, reptiles keep their body temperature from varying with environmental temperature, by maintaining it at a certain level within this 50°C span. Evolutionarily, reptiles can choose the ceiling of their preferred range by behaviorally utilizing solar energy. Empirical evidence of this is the occupation by several species of reptiles with different PBTs of a common habitat (Cowles and Bogert, 1944; Bogert, 1959; Soulé, 1963). However, the thermal characteristics of the environment leave less evolutionary choice in the lower threshold of the PBT because reptiles lack the cooling mechanisms characteristic of most mammals and birds (Schmidt-Nielsen and Dawson, 1964) and can therefore cool only to the level of the coolest segment of their environment. Summer shade temperatures in North America set this lower utilizable

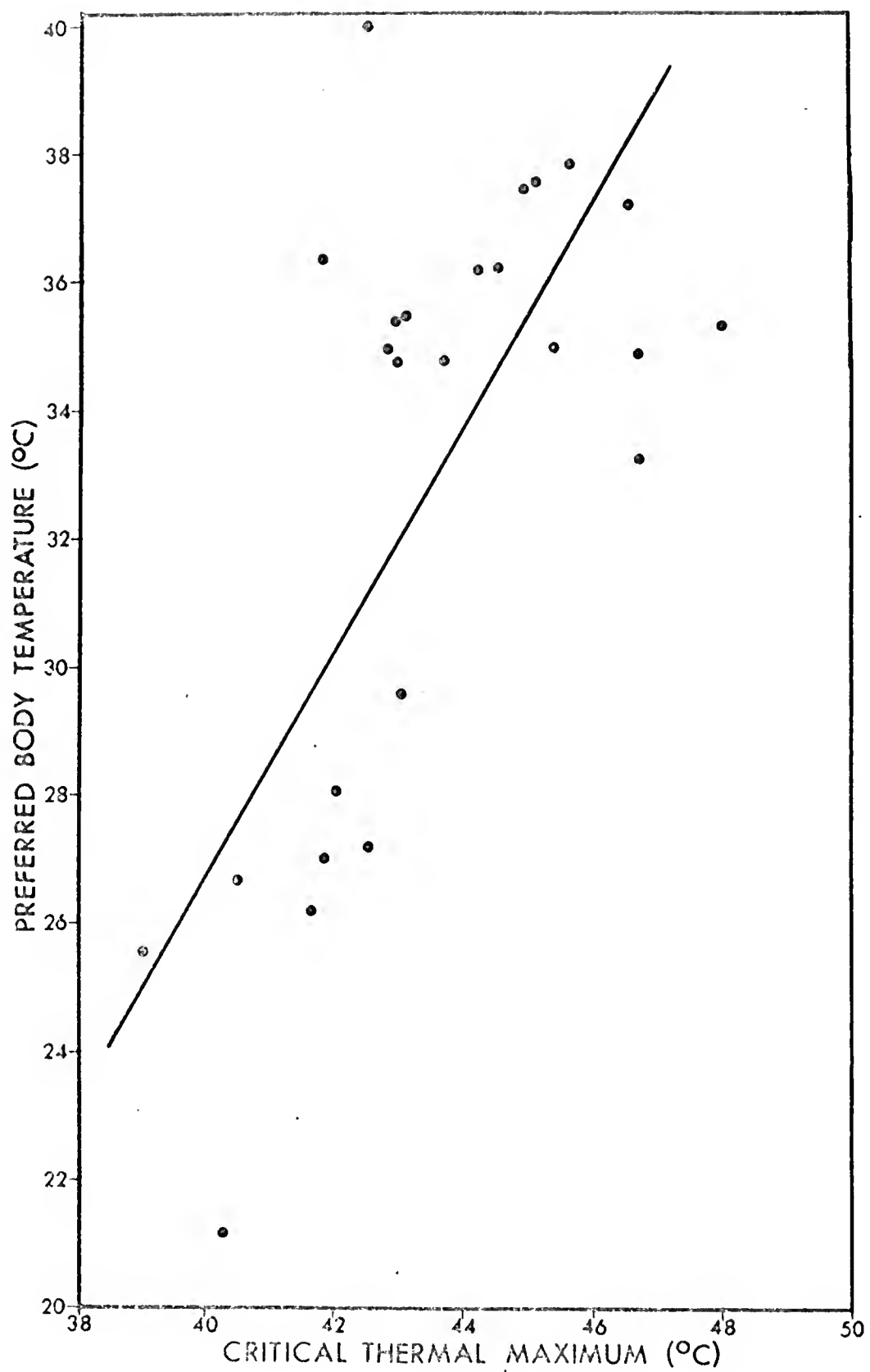
level at about 20°C to 23°C for diurnally-active terrestrial reptiles. Thus, the observation that PBT is generally closer to the critical thermal maximum¹ than to the critical thermal minimum² is to be expected, because the thermal range between critical thermal minimum and $20\text{-}23^{\circ}\text{C}$ is unavailable. However, many diurnal reptiles operate at thermal levels only a few degrees below temperatures that cause irreversible tissue damage. The question, therefore, becomes why do not all diurnally active reptiles choose PBTs of about $25\text{-}35^{\circ}\text{C}$ and leave margins of safety at both ends? The answer is apparently related to (1) the biological effects of thermal extremes and (2) the correlation between PBT and the critical thermal maximum.

Hypothermia slows the rates of physiological processes, but rarely causes irreversible damage above 0°C . However, irreversible tissue damage is incurred at temperatures above about 44°C . These temperatures slightly exceed the highest air temperature (though certainly not the highest black-bulb temperature) to which a diurnal animal could expect to be exposed in its normal activity and natural habitat. There is a direct correlation between the preferred level of body temperature and the level of critical thermal maximum (Schmidt-Nielsen and Dawson, 1964; Brattstrom, 1965; see Fig. 18). The highest body temperature a reptile will ever attain must be below the CTMax if that animal is to survive, and this body temperature should be directly related to the highest air temperature experienced. These environmental thermal extremes are

¹"The thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death" (Cowles and Bogert, 1944).

²"The temperature that causes a cold narcosis and effectually prevents locomotion" (Cowles and Bogert, 1944).

Figure 18. The relationship between preferred body temperature and critical thermal maximum in reptiles ($r^2 = .59$) Data are from Brattstrom (1965) for species with sample sizes of 20+.



selective factors which set the level of CTMax by eliminating the individuals with lowest thermal tolerance. Since CTMax bears a relationship to PBT, that is apparently genetically fixed, there should be a direct correlation between these environmental extremes and PBT. Furthermore, the PBT of a reptile should be more strongly correlated with the highest temperature recorded in its habitat than with any mean high temperature value because the latter are clearly of less evolutionary significance in fixing the level of CTMax.

Figure 19 shows the high correlation ($r^2 = 0.61$) between PBT in several primarily heliothermic³ species of reptiles and the highest temperature ever recorded at the weather station nearest the collection locality (Kincer, 1941). Studies that failed to list collecting locality, or for which no such weather data could be found, are excluded. Data from studies in which field body temperatures constituted the basis for determination were included only if the sample size exceeded 20 and observational correlations were made. When these conditions are met, PBT and mean body temperature (Peters, 1964) become synonymous and comparison between these values is valid. The pertinent statistical data and references are listed in Table 3.

As expected, the correlation with PBT is significantly greater for maximum temperature than for the mean temperature of the hottest month (July in the northern hemisphere, January in the southern). This supports the hypothesis that the level of PBT is indirectly fixed evolutionarily by its relationship to the level of CTMax, which is directly fixed by high environmental temperature extremes. This does

³ A primary heliotherm is here defined as a diurnally-active lizard inhabiting an open habitat (or habitats) that offer access to sunlight throughout the day.

Figure 19. Relationship between preferred body temperature of primary heliotherms and the highest air temperature recorded in the area from which they were collected. Statistical information and sources for the data are listed in Table 3.

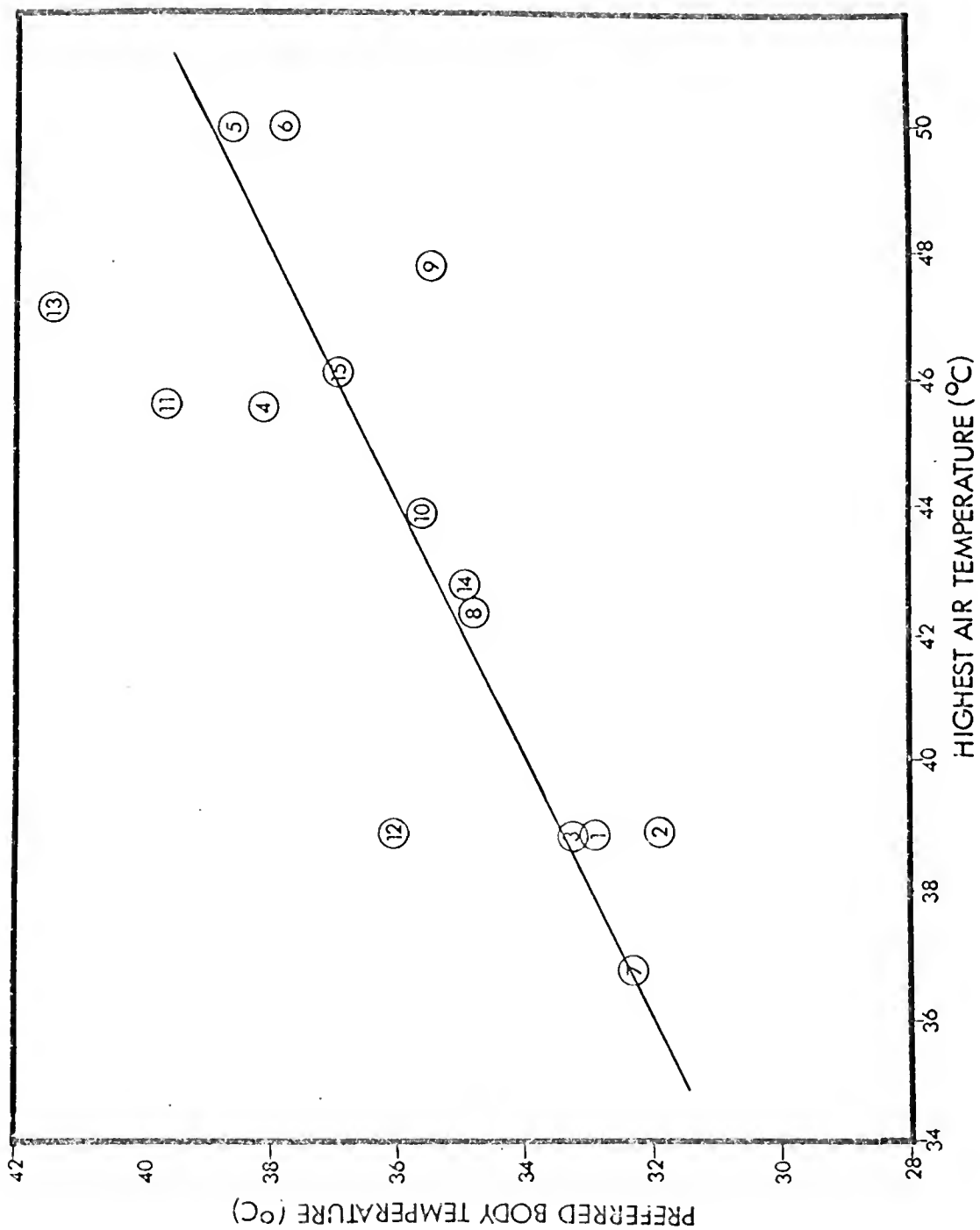


Table 3. Data for points plotted in Figure 19 for primary heliothermic lizards.

NUMBER IN FIG. 19	SPECIES	N	PBT	SOURCE
1	<u>Anolis allisoni</u>	122	33.0	Ruibal, 1961
2	<u>Anolis homolechis</u>	104	31.8	Ruibal, 1961
3	<u>Anolis sagrei</u>	178	33.1	Ruibal, 1961
4	<u>Crotaphytus collaris</u>	425+	38.0	Fitch, 1956
5	<u>Dipsosaurus dorsalis</u>	M*	38.5	DeWitt, 1967b
6	<u>Sauromalus obesus</u>	49	37.7	Cowles and Bogert, 1944
7	<u>Sceloporus graciosus</u>	70	32.3	Mueller, 1969
8	<u>Sceloporus occidentalis</u>	500+	35.0	Larson, 1961
9	<u>Sceloporus orcutti</u>	21	35.4	Mayhew, 1963
10	<u>Urosaurus ornatus</u>	97	35.5	Brattstrom, 1965
11	<u>Cnemidophorus sexlineatus</u>	M*	39.5	Fitch, 1956
12	<u>Sceloporus woodi</u>	42	36.0	Bogert, 1949
13	<u>Cnemidophorus tesselatus</u>	33	41.3	Bogert, 1949
14	<u>Amphibolorus barbatus</u>	58	34.8	Lee and Badham, 1963
15	<u>Amphibolorus inermis</u>	M	36.8	Pianka, 1971

MAXIMUM TEMP.

MEAN HIGH TEMP.

CORRELATION COEFFICIENT

0.78

0.54

EQUATION FOR LINE

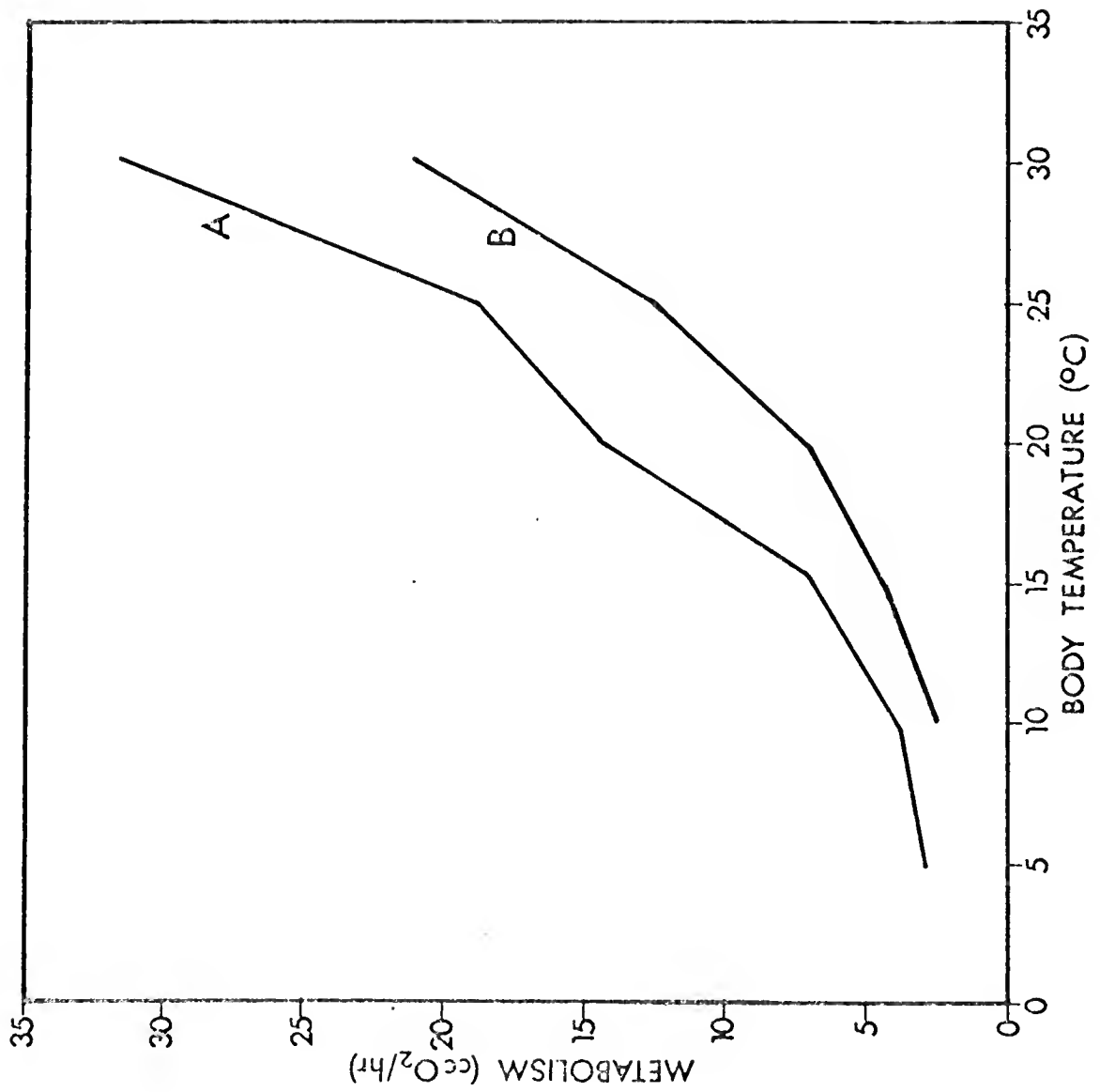
$Y = .492X + 14.46$

*many

not mean, however, that the absolute level of PBT is solely a function of high air temperature extremes. Any species-specific behavior (burrowing, panting, etc.) that meliorates the severity of such extremes will be of selective advantage. It is the interaction of these behavior patterns and physiological tolerances that, under the selective pressures of high temperatures, will determine the level of PBT. Interspecific differences in behavior and physiological tolerance will result in the utilization by several species with slightly different PBTs of a common habitat.

By setting their body chemistry to operate optimally at a given temperature, reptiles concomitantly must accept diminished levels of 'metabolic efficiency' at non-optimal temperatures. At body temperatures below PBT, metabolism merely slows down as a function of temperature (Fig. 20), and normal activity, such as food procurement, ceases. But, at such times, the animal incurs no tissue damage and the decreased level of metabolism is compatible with decreased digestive efficiency (and therefore energy availability) and food consumption. At temperatures above PBT, however, the decreased levels of digestive efficiency (and metabolic efficiency generally) and food consumption coincide with an increase in metabolism. In addition, very high temperatures will cause irreversible tissue damage. So by choosing relatively high body temperatures, heliothermic reptiles avoid the problem of overheating and are penalized by having to remain inactive or suboptimally active on cool days. The opposite strategy of choosing a low PBT to insure more days of activity entails the risk of overheating to the point of death. This, as mentioned, is probably the mechanism that sets the level of reptilian PBT evolutionarily. High thermal extremes will eliminate the least heat tolerant (lowest CT_{Max})

Figure 20. The effect of temperature on the metabolic rate of a 509 g Natrix taxispilota at two acclimation temperatures, (A) 20° and (B) 25°.



individuals and select for a species with a higher CTMax (and PBT). Theoretically, a reptile's CTMax should be just above the highest ambient temperature (and body temperature) the species ever encountered in its normal habitat during its normal period of activity. Therefore, diurnal terrestrial species should have higher PBTs than nocturnal terrestrial species.

Still, the highest daytime air temperature recorded in an area should be correlated with the highest night temperature. A correlation, then, does exist between PBT of nocturnal reptiles and highest air temperature (Fig. 21). The correlation is weaker than with primarily heliothermic species, as would be expected. Between the lines relating PBT with highest air temperature in primary heliothermic species and in nocturnal species, there are a series of points which form a third line with an intermediate slope. The points are for diurnally-active snakes and forest lizards. The lizards (Anolis and Eumeces) bask (in patches of sunlight reaching the forest floor) but not nearly as extensively as primary heliothermic species. However, the heliothermic snakes (Coluber and Heterodon) occur in the same open habitats in which heliothermic lizards maintain higher PBTs. This suggests that the differences in thermal preferenda of snakes and lizards may be a function of differences in the ecology of the two groups. The nocturnal species used to determine line A (Fig. 21) were, with one exception (the Gila monster, Heloderma suspectum), all snakes, so it is impossible to determine from these data whether their lower thermal preferenda exist because they are nocturnal or because they are snakes, or both.

One consistent characteristic of snakes that separates them from almost all lizards suggests a basis for a lower PBT. This is the absence of legs. The thermoregulatory significance of this is that

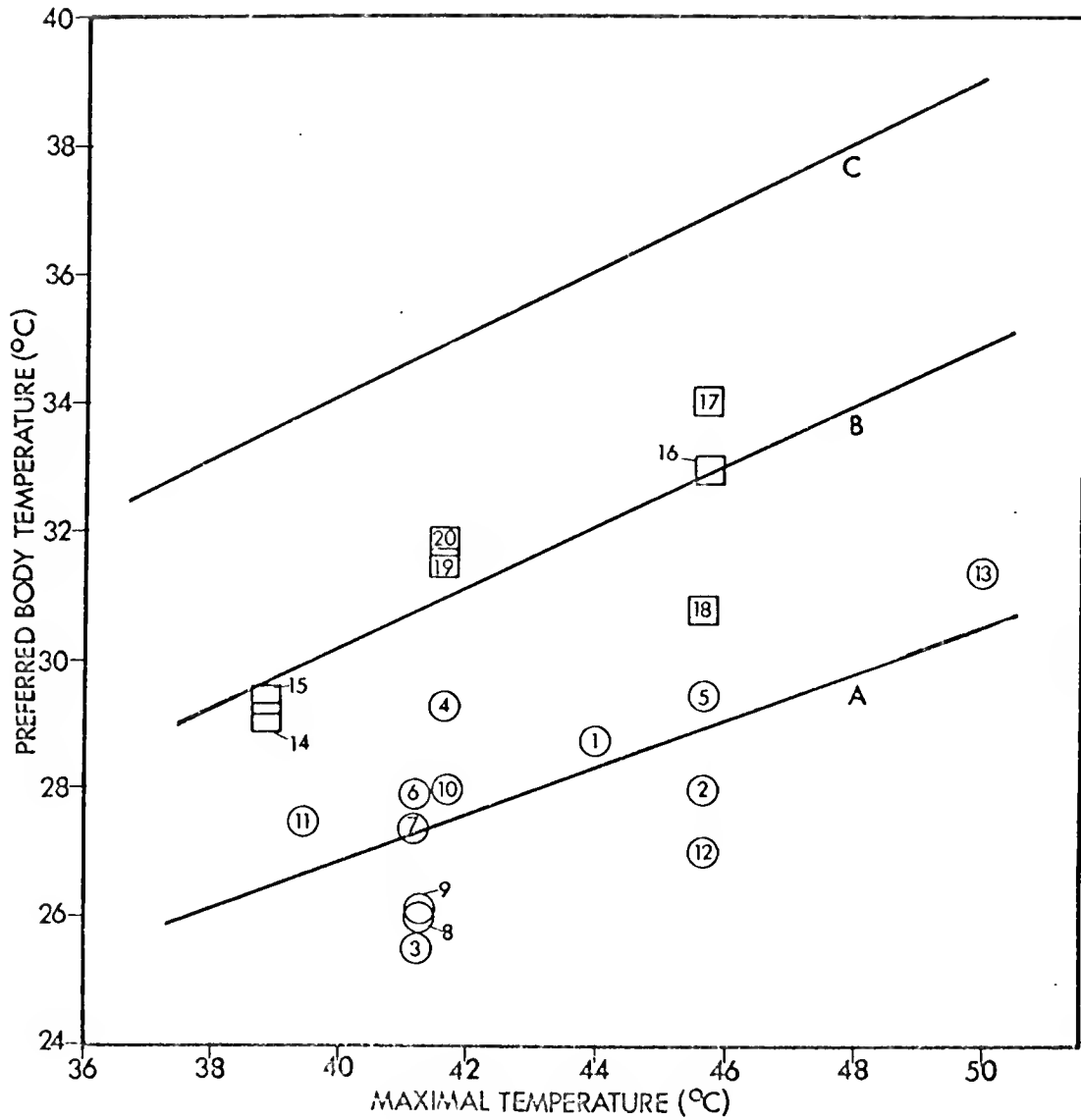


Figure 21. Relationship between reptilian preferred body temperature and the highest air temperature recorded in the collection area. A. nocturnal reptiles (circles). B. diurnal snakes and forest lizards (squares). C. primary heliothermic lizards (from Figure 17). Statistical information and sources for data are listed in Table 4 (line A) and Table 5 (line B).

Table 4. Data for points plotted in Figure 21 for nocturnal reptiles (line A).

NUMBER IN FIG. 21	SPECIES	N	PBT	SOURCE
1	<u>Heloderma suspectum</u>	57+	28.7	Bogert and del Campo, 1956
2	<u>Elaphe obsoleta</u>	53	28.0	Fitch, 1956
3	<u>Thamnophis sirtalis</u>	157	25.6	Carpenter, 1956
4	<u>Thamnophis sirtalis</u>	108	29.3	Kitchell, 1969
5	<u>Thamnophis sirtalis</u>	21	29.5	Fitch, 1965
6	<u>Thamnophis sirtalis</u>	M	28.0	Stewart, 1965
7	<u>Thamnophis ordinoides</u>	M	27.4	Stewart, 1965
8	<u>Thamnophis sauritus</u>	123	26.0	Carpenter, 1956
9	<u>Thamnophis butleri</u>	54	26.1	Carpenter, 1956
10	<u>Natrix sipedon</u>	114	28.0	Kitchell, 1969
11	<u>Natrix taxispilota</u>	48	27.5	Present paper
12	<u>Ancistrodon mokeson</u>	73	27.0	Fitch, 1956, 1960
13	<u>Crotalus cerastes</u>	M	31.4	Cowles and Bogert, 1944

	MAXIMAL TEMP.	MEAN HIGH TEMP.
CORRELATION COEFFICIENT	0.68	0.65
EQUATION FOR LINE	$Y = .368X + 12.07$	----

Table 5. Data for points plotted in Figure 21 for diurnal snakes and forest lizards (line B).

NUMBER IN FIG. 21	SPECIES	N	PBT	SOURCE
14	<u>Anolis</u> <u>allogus</u>	148	29.2	Ruibal, 1961
15	<u>Anolis</u> <u>lucius</u>	86	29.3	Ruibal, 1961
16	<u>Eumeces</u> <u>fasciatus</u>	41+	33.0	Fitch, 1954, 1956
17	<u>Eumeces</u> <u>obsoletus</u>	M	34.0	Fitch, 1955
18	<u>Coluber</u> <u>constrictor</u>	29	30.9	Fitch, 1956
19	<u>Coluber</u> <u>constrictor</u>	127	31.5	Kitchell, 1969
20	<u>Heterodon</u> <u>platyrhinos</u>	102	31.8	Kitchell, 1969

	MAXIMUM TEMP.	MEAN HIGH TEMP.
CORRELATION COEFFICIENT	0.81	0.48
EQUATION FOR LINE	$Y = 0.344X + 40.27$	----

terrestrial snakes are in more intimate physical contact with their environment and more vulnerable to conductive heat exchange with the substrate. This, in part, explains why Carpenter (1956), in his study of thermoregulation in three species of garter snakes, found cloacal temperatures to be more closely correlated with the temperature at the ground surface than with air temperature above or soil temperature below. Desert lizards rely greatly on such conductive heat exchange as a cooling mechanism. The desert iguana, Dipsosaurus dorsalis, presses its venter from side to side in the sand exposing cooler layers to which it loses body heat by conduction (Norris, 1953). At higher temperatures, lizards retreat to burrows (DeWitt, 1967a, 1967b; McGinnis, 1967; Norris, 1953) again relying on conductive heat exchange to reach the preferred thermal level. The high surface temperatures characteristic of desert regions frequently exceed the preferred body temperatures of the reptiles occurring there. While a heliothermic tetrapod can hold its body above this substrate and thermoregulate with a degree of independence of it, snakes cannot. This undoubtedly at least partly accounts for the paucity of diurnally active snakes in desert areas where lizard species are abundant. And a nocturnal activity pattern preordains a relatively low PBT.

If the absence of legs is of significance in determining the level of PBT, diurnally-active legless lizards should fall on line B (Fig. 21) with diurnal snakes. The only data available for such lizards are for the species Ophisaurus attenuatus (Fitch, 1956) in Kansas. Field temperatures of 15 active individuals collected on clear days ranged between 30.6°C and 33.7°C. The mean value of 32.2°C would fall 1.4°C below the diurnal snake-forest lizard line. This is good agreement even though this point was based on a sample size too small to warrant its inclusion in Fig. 21.

SUMMARY

1. Thermoregulatory behavior under natural and laboratory conditions was studied in the brown water snake Natrix taxispilota.
2. The effect of temperature on digestive extraction efficiency was determined calorimetrically.
3. The effect of acclimation on metabolic rate and preferred body temperature was determined.
4. There is an inverse relationship between preferred body temperature and acclimation temperature in brown water snakes. A seasonal change in preferred body temperature occurs in nature.
5. There is an inverse relationship between thermal level of acclimation and metabolic rate at a given temperature. Metabolism becomes acclimated to the highest of varying temperatures to which the snake is exposed in a 24-hour period.
6. There are lower air and water threshold temperatures for emergence in brown water snakes. Factors affecting the levels of these thresholds include thermal acclimation and physiological state of the animal.
7. Natrix taxispilota will not emerge at any air and water temperatures in the absence of light.
8. There are temporal changes in the propensity for emergence after initial onset of light.
9. Thermoregulatory responses of brown water snakes to various thermal regimes are described and discussed.
10. There is a temperature-independent evening submergence response in Natrix taxispilota.

11. Brown water snakes digesting food thermoregulate at a sub-level within the normal preferred body temperature range.
12. Digestive efficiency is greatest at about 30°C and decreases above and below this level.
13. It is suggested that high thermal extremes directly fix the critical thermal maximum of reptiles and indirectly fix the preferred body temperature. Supportive evidence is presented and discussed.
14. The absence of legs in snakes precludes thermoregulation with the degree of independence of conductive heat exchange with the substrate enjoyed by most lizards. It is suggested that this may, in part, account for the relatively low preferred body temperatures of snakes.

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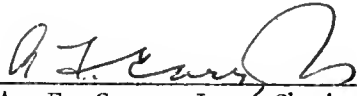
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BIOGRAPHICAL SKETCH

Donald Eugene Goodman was born January 30, 1944, at Kennett, Missouri. In June, 1966, he received the degree of Bachelor of Arts with a major in Zoology from the University of Missouri. In 1966, he enrolled in the Graduate School of the University of Florida and has until the present time pursued his work toward the degree of Doctor of Philosophy in the Department of Zoology.


Donald Eugene Goodman is a member of the American Society of Ichthyologists and Herpetologists and the American Association for the Advancement for Science.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



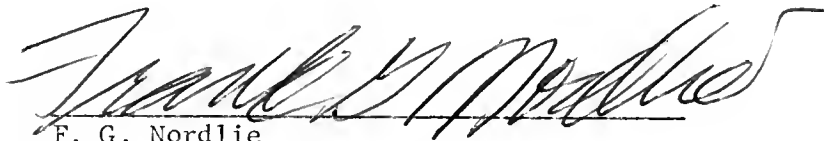
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B. K. McNab, Co-Chairman
Associate Professor of Zoology

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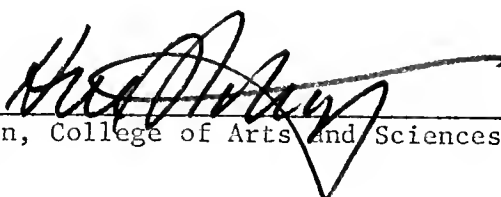
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This dissertation was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June, 1971



Dean, College of Arts and Sciences

Dean, Graduate School



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